SPATIAL MATTERS

HOW SPATIAL PROCESSES & PATTERNS AFFECT SAVANNA DYNAMICS

Thomas A. Groen

SPATIAL MATTERS

HOW SPATIAL PATTERNS & PROCESSES AFFECT SAVANNA DYNAMICS

Promotor: Prof. dr. Herbert H.T. Prins
Hoogleraar Resource ecology

Co-promotoren: Dr. ir. Frank van Langevelde
Universitair docent, leerstoelgroep Resource ecology
Dr. Claudius A.D.M. van de Vijver
Staflid PE&RC

Promotiecommissie:

Prof. dr. K.E. Giller	Wageningen Universiteit
Prof. dr. M. J.A. Werger	Universiteit Utrecht
Dr. J. Gignoux	Ecole Normale Supérieure, Paris, France
Prof. dr. F. Jeltsch	Universität Potsdam, Germany

Dit onderzoek is uitgevoerd binnen de onderzoeksschool PE&RC

SPATIAL MATTERS

HOW SPATIAL PATTERNS & PROCESSES AFFECT SAVANNA DYNAMICS

Thomas A. Groen

Proefschrift
ter verkrijging van de graad van doctor
op gezag van de rector magnificus
van Wageningen Universiteit
prof. dr. M.J. Kropff,
in het openbaar te verdedigen
op woensdag 5 september 2007
des namiddags te 13:30 in de Aula

[redacted]

Groen T.A.
Spatial matters: how spatial patterns & processes affect savanna dynamics
Wageningen University, the Netherlands
PhD thesis (2007); ISBN 978-90-8504-690-5

Table of contents

CHAPTER 1
General introduction 1

CHAPTER 2
Correlations between tree patterns in African savannas and top-down and bottom-up factors: a continental analysis 7

CHAPTER 3
Clustering of savanna trees reduces damaging effects of fire in south african savannas (submitted) 23

BOX 3.1
The interaction between the diameter of clusters of woody species and fire intensity 35

CHAPTER 4
Herbivores as architects of savannas: inducing and modifying spatial patterning (submitted) 41

CHAPTER 5
Spatial patterns in savanna trees and grasses due to herbivory 57

CHAPTER 6
Dynamic interactions between vegetation and herbivore populations increase the stability of savannas (submitted) 73

CHAPTER 7
The spatial scale of fire influences the stability of savanna ecosystems 85

CHAPTER 8
Synthesis: the effects of spatial patterns & processes 101

Summary 111

Samenvatting 115

Acknowledgements 119

Affiliation of authors 121

Curriculum vitae 123

List of publications 125

PE&RC PhD Education Certificate 127

References 129

Abstract

Groen T.A., 2007. Spatial matters: how spatial processes & patterns affect savanna dynamics.

This thesis investigates the role of fire and herbivory as spatial processes determining savanna dynamics, and especially the effect on the occurrence of bush encroachment. Fire can create spatial heterogeneity by inducing clustering of trees, which then experience less damage from fires than solitary trees. Herbivory can also create spatially heterogeneity through two processes: (1) self facilitation — where herbivores improved the quality of forage through consumption — and (2) spatially explicit grazing — where patch selection is based on the average quality of the environment. This spatial heterogeneity of the vegetation is an important feature that prevents the occurrence of sudden shifts from a state with both trees and grasses towards an alternative state with tree dominance and no grasses. When savannas are spatially heterogeneous, they respond gradually to changes in herbivory levels rather than displaying these sudden shifts. Heterogeneous systems will respond to both increasing and decreasing grazing pressure with a gradual decrease and increase in grass abundance, respectively. In heterogeneous vegetation sudden shifts do occur in small patches with grass dominance, but averaged over the whole system these shifts are levelled out. However, once savannas become dominated by trees, they lose their heterogeneity. Then the system as a whole is able to shift towards a state with both trees and grass only when grazing pressure is decreased below a threshold value, and fires occur regularly. This thesis therefore concludes that heterogeneous savanna vegetation, induced by fire and herbivory, prevents sudden bush encroachment.

Keywords*: savanna, spatial heterogeneity, alternative stable states, ecosystem shifts, bush encroachment, spatial ecology, herbivory, fire.*

CHAPTER 1
General introduction

Spatial patterns are thought to play a decisive role in the functioning of terrestrial systems that are known for their spatially heterogeneous physiognomy (Rietkerk *et al.* 2004). For example, desertification in arid areas is prevented by the existence of patches of grassy vegetation. Indeed, within current day ecology, a growing awareness appears on the role that spatial processes play in these systems (Tilman & Kareiva 1997, Fortin & Dale 2005). In this respect important questions are raised such as, "How do ecosystems become spatially heterogeneous?", and "What are the effects of spatial heterogeneity on processes in the system?"

Now that 'space' has been identified as a crucial factor in the structure and dynamics of heterogeneous ecosystems, these are prime questions to be answered to be able to provide reliable explanations of ecosystem behaviour, to help to mitigate current ecological problems, and to predict and maybe even prevent possible future problems. In this thesis I try to address these questions while looking at tree grass interactions in savannas.

Space in ecology

Spatial interactions in ecological systems have already been under study for several years, and one of the first questions needed to be answered was "does space matter?" Tilman and Kareiva (1997) stated that "Space may not always matter, but when it does matter, to neglect it could produce major misunderstandings". This means that we need to know whether spatial interactions are important, and to what extent they influence ecosystem processes. An indication of when space matters in ecology was given by Law *et al.* (2000) who stated that mean field approaches may only be assumed when ecological processes maintain homogeneity in ecosystems (physical forces cause strong mixing of the system, organisms in the system are highly mobile, or individual organisms interact over long distances). When the conditions in an ecosystem deviate from these, applying mean field approaches become less suitable, and application of more sophisticated spatial techniques are required. Important progress has been made in recent years to understand how individual organisms interact in spatial environments. For example, the consequences of limited dispersal of plants on their direct intraspecific competitive interactions have well been investigated (Tilman *et al.* 1997).

Another aspect in spatial ecology which is relatively new and certainly needs further insight is the effect of space on ecosystem response to environmental change, especially the stability of ecosystems (Rietkerk *et al.* 1996, 2004, Van Nes & Scheffer 2005). For example, the interplay between run-off of water from bare patches and the run-on of water on vegetated patches has important consequences for the stability of arid grazing systems (Van de Koppel & Rietkerk 2004). Observations of sudden shifts in ecosystems have urged ecologists to provide plausible explanations for the mechanisms behind these shifts, and to provide indications of the resilience of ecosystems against these shifts. The assessment of the resilience of ecosystems in a spatial context can be challenging, but is very relevant in the light of the present reality of increasing human pressure and climatic change. This is especially the case for ecosystems such as savannas that are expected to be among the most sensitive for land use and climatic changes (Sala *et al.* 2000, Bond *et al.* 2003).

Ecosystem shifts

The generic mechanism behind the occurrence of sudden shifts in dynamics systems (such as ecosystems) is not new, and date back to the formulation of catastrophe theory by Thom (1975). The mechanism behind catastrophe theory is fairly straightforward and best explained using an illustration as in Figure 1.1. Although we will introduce savannas in the next section,

we will discuss the theory making use already of savannas, where both trees and grasses compete for the same resource, water. We will consider the fate of the equilibrium grass biomass as a function of two determining factors, precipitation and fire frequency. Figure 1.1A displays the equilibrium amount of grass biomass as a folded plane in a three dimensional space with precipitation and fire frequency along the two horizontal axes and equilibrium grass biomass on the vertical axis.

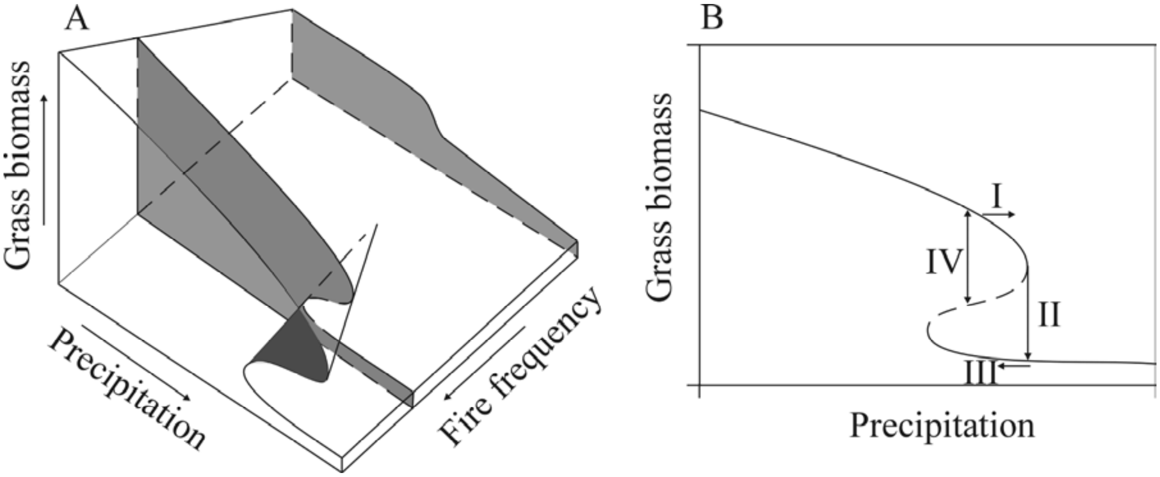


Figure 1.1 An example of the cusp catastrophe model (A) and a more detailed image of the dashed cross-section (B), for the savanna ecosystem. The folded plain in A and the solid line in B represent stable equilibrium grass biomass values in the savanna ecosystem under different values of precipitation and fire frequency. Because of the fold in the system, under some combinations of precipitation and fire frequency, more then one equilibrium exists, so called alternative stable states. The dashed line in B represents an unstable equilibrium of grass biomass, and this line acts as a boundary between the upper and lower stable states. For further explanation, see text.

Systems often show a gradual response to changing environmental conditions. In savannas, with increasing precipitation, trees become more and more abundant, suppressing grass biomass (Walker & Noy-Meir 1982), resulting in a reduced equilibrium grass biomass. Therefore, the equilibrium grass biomass decreases continuously with increasing precipitation at low levels of fire frequency (Figure 1.1A, the back plane of the figure). However, at higher levels of fire frequency a continuous increase in precipitation can lead to a discontinuous change in grass biomass (Cross section of Figure 1.1A and Figure 1.1B). In savannas, a small and continuous increase in precipitation (arrow I, Figure 1.1B) can lead to a discontinuous decrease in grass biomass (arrow II, Figure 1.1B) when fire frequency is high, but not when fire frequency is low (Van Langevelde *et al.* 2003). Such a discontinuous change is called a *catastrophic shift*. Once the system is shifted to the new situation (*i.e.*, a lower grass biomass in our example), a reduction back to the previous level of precipitation (arrow III, Figure 1.1B) does not lead to a restoration of the system to its initial grass biomass level, but the system remains at the new low value. This phenomenon is known as *hysteresis*. Only with a very strong reduction in precipitation will the system return to its initial value of high grass biomass.

Not only a change in environmental conditions can cause a (catastrophic) shift, also a disturbance can cause such a shift. The fold displayed in Figure 1.1A consists of both stable and unstable states, as can be better seen in Figure 1.1B (dashed vs. solid lines). The unstable state acts as a boundary between the different stable states. When the system is pushed by a disturbance over this border, the system will not return to its original equilibrium, but will shift to the alternative equilibrium. When, in savannas, the ecosystem is in the upper stable state and a certain amount of grass biomass is removed by grazing, but the remaining amount of grass biomass remains above this unstable equilibrium, it will return to its previous stable state. However, when the remaining amount of grass biomass is below the unstable equilibrium, the system will shift to the lower stable state. The disturbance the system can handle without shifting to a different stable state is termed the *resilience* of the system (arrow IV, figure 1.1B).

An important mechanism that can cause systems to behave as described above is the existence of *positive feedbacks*. *Positive feedbacks* are mechanisms that reinforce themselves. In savannas for example, grasses are the main fuel for fires determining the intensity of fire, although grasses hardly suffer from burning, depending on the season (Van de Vijver 1999, De Ronde 2004). Trees on the other hand are damaged by fires, and more intense fires cause more damage than less intense fires. This can constitute a *positive feedback* (Van Langevelde *et al.* 2003). When sufficient grass biomass is available (above the dashed line in Figure 1.1B), fires are severe, suppress tree growth, and indirectly reduce competition of trees with grasses for water. Therefore, grasses will perform better, produce more biomass, causing even more intense fires, and so on. Also, when insufficient grass biomass is available (below the dashed line in Figure 1.1B), fires are less intense and trees will perform better, increasing competition with grasses for water. As a result, grasses will perform less well, producing less grass biomass, resulting in less intense fires and so on. The unstable equilibrium in Figure 1.1B is a border above which the positive feedback between grass biomass, fire intensity and tree damage acts in favour of grass, while below it, the same *positive feedback* acts in favour of tree biomass.

In Figure 1.1B, in the area where the unstable equilibrium is present (the dashed line) also two stable equilibria exist (the solid lines). When two stable equilibria exist under the same environmental conditions (in our case with equal amounts of precipitation), we speak of *alternative stable states*. When *alternative stable states* are present in an ecosystem, is can display sudden (catastrophic) shifts from the one state to the other. The probability of a sudden shift in an ecosystem is determined by the distance the system is away from the point at which a *catastrophic shift* can occur (arrow II, Figure 1.1B), the variability in the environmental conditions (arrow I, Figure 1.1B), the *resilience* of the system (arrow IV, Figure 1.1B) and the amount of disturbance to which the system is exposed.

Although Zeeman (1967) already stressed the application of catastrophe theory in ecological systems, an analysis of predator prey-graphs by Noy-Meir (1975) and further investigation of his ideas by May (1977) launched the interest of other ecologists in the possibilities of sudden shifts in grazing ecosystems. The implications of *catastrophic shifts*, *hysteresis* and *resilience* have since been discussed for several ecosystems, including shallow lakes, arid grazing systems and savannas (Rietkerk & Van de Koppel 1997, Van de Koppel *et al.* 1997, Scheffer *et al.* 2001, Van Langevelde *et al.* 2003, Schröder *et al.* 2005). In this thesis, I will investigate the effects of spatial processes on the occurrence of sudden shifts in savannas.

The savanna ecosystem

Savannas are typically spatially heterogeneous ecosystems that are characterised by a continuous grass layer and scattered tree growth (Scholes & Archer 1997). Because savannas are subject to high spatial and temporal variation in environmental conditions and human pressure, they form a good system to study the importance and impact of spatial interactions.

The savanna ecosystem was long perceived as a transition zone between the grassland and woodland ecosystem, which seems an undervaluation as they cover approximately 12% of the global land surface and harbour around a fifth of the human population (Scholes & Archer 1997). Many of those who live in the savanna ecosystem depend on its primary and secondary production. In order to secure the livelihood of those depending on savannas, a functional understanding of the mechanisms that keep the savanna ecosystem from developing into either grassland or woodland is essential. Especially determining mechanisms that are or can be controlled by man such as fire, livestock and wildlife densities are crucial to understand in this respect, to accordingly come up with sustainable management strategies for these systems.

Savanna dynamics

In savannas changes in tree and grass abundance occur. Some authors suggest that the savanna is not a stable mixture of trees and grasses, but an unstable mixture persisting due to processes like herbivory, fire and fluctuating rainfall (Scholes & Walker 1993, Jeltsch *et al.* 2000, Sankaran *et al.* 2005), while other authors describe changes in savannas as single events with marked effects on the functioning of the savanna ecosystem. Many of these studies describe the transformation of savannas with tree-grass co-dominance towards a tree or shrub dominated system (Archer *et al.* 1988, Briggs *et al.* 2002, Brown & Carter 1998, Roques *et al.* 2001, Van Auken 2000), although examples of the inverse direction are available (*e.g.*, Dublin *et al.* 1990, Hoffmann *et al.* 2002)

A system with a substantial grass component is often preferred from a cattle raising point of view. Therefore much research has been performed on the processes that lead to a sudden increase in tree dominance, also termed bush encroachment and how to prevent such a shift (Gillson & Hoffman 2007, Janssen *et al.* 2004, Van Langevelde *et al.* 2003). The processes responsible for these dynamics of savannas include herbivory and the occurrence of fire (Scholes & Archer 1997) as changes in these processes can lead to bush encroachment under certain conditions of rainfall and bush encroachment. (Van Langevelde *et al*. 2003). These processes affect the tree grass balance through a variety of direct and indirect effects (Figure 1.2). However, it should also be realised that both fire and herbivory are spatial processes. Herbivores have to select locations where they forage, and through that automatically leave other places undisturbed, creating spatial differences in levels of disturbance over space and time (Adler *et al.* 2001, Cid & Brizuela 1998). Fires are typically started at a single location, and only affect other locations by spreading through the area to those locations. Whether fires will reach those other locations, and with which intensity, depends on the spatial distribution of fuels (Berjak & Hearne 2002). Therefore, it is important to know if and how fire and herbivory can shape or change spatial patterns in savannas and how they are influenced themselves by spatial patterns. Fire and herbivory are of importance to study, because they, in turn, can be managed by humans, and therefore are important management tools in savannas.

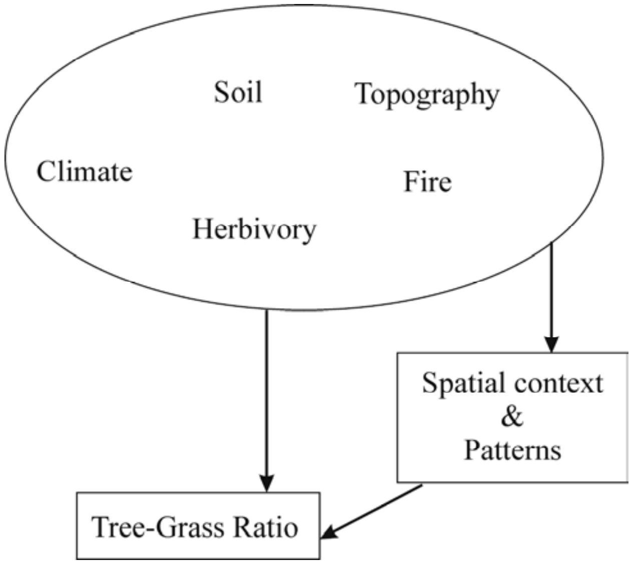


Figure 1.2 The direct and indirect effects of different processes on the tree-grass ratio in savanna ecosystems.

Outline of the thesis

In this thesis, I deal with a spatially heterogeneous ecosystem that is capable of displaying alternative stable states and which is subjected to temporally and spatially variable conditions, like the occurrence of fire and herbivory. It therefore is an ideal system to investigate the questions whether spatial processes affect ecosystem stability and how the processes are affected by system heterogeneity. In this thesis I study if and how fire and herbivory can shape or change spatial patterns and how they are influenced themselves through spatial patterns. We will focus on three specific research questions for savanna ecosystems:

1-"What is the effect of spatial heterogeneity on spatial processes?"
2-"How is spatial heterogeneity created by spatial processes?" and
3-"Is the occurrence of sudden ecosystem shifts influenced by these spatial patterns and processes?"

It is important to realize what is meant by the terms pattern, because it is a broad and general term that can be interpreted in many ways. In this thesis the term pattern will be used to describe the non homogeneous, non random spatial organisation of trees and grasses. In the following chapters I will look at different aspects of savanna dynamics making use of both empirical data and modelling techniques. Figure 1.3 shows how the different chapters fall within the general structure of the model.

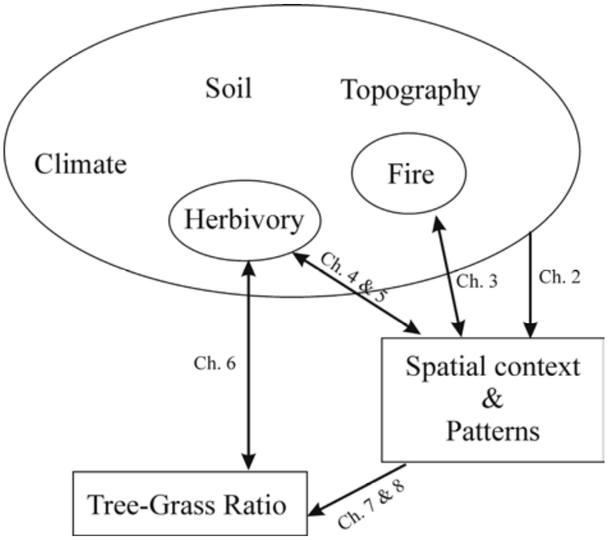


Figure 1.3 Schematic representation how different chapters in the thesis relate to the processes that are investigated in this thesis. Single arrows indicate "effects of" and double arrows indicate interactions.

In chapter 2 I analyse the correlation between spatial processes and spatial patterns in savannas. This chapter helps in defining which processes are of importance for determining spatial patterns in savannas. In this chapter we look at a continental scale which factors are best correlated with patterns in savannas. To this end we use aerial photography, taken over a great variety of sites throughout the African continent, and quantify patterns in terms of tree pattern indices

In chapter 3 I investigate the interaction between spatial pattern and fire to address the first research question of this thesis. We investigate how the spatial pattern in trees can reduce the negative effect of fire on trees. Also, we investigate how tree patterns are influenced by fire. In line with the second research question of this thesis, we investigate how fire can act as a clustering agent in savanna trees using a unique burning experiment in the Kruger Park, which has been running for at least 50 years. In addition to the effect of tree clusters on the negative effects of fire, as found in the experimental burning plots, we describe further research on the effects of bush cluster size on fire intensity in a separate Box (Box 3.1) . Here we report on an experimental setup where we vary bush cluster sizes and measure the intensity of fires on the leeward and windward sides of these clusters.

In chapter 4 I investigate what the consequences of spatially heterogeneous herbivory are for savanna patterns, which relates to the second research question of this thesis. We look at the formation of tree grass patterns through the interaction between herbivores and vegetation making use of Gierer-Meinhardt type models (Gierer 1981, Meinhardt 2003). We model the distribution of herbivore pressure in a spatially heterogeneous environment. We investigate how interactions between forage availability and herbivore pressure can result in spatial patterns. Making use of Turing stability analysis we can make predictions under which conditions spatial patterns can occur. This can yield new insights in the spatial dynamics of savannas and help us formulate new hypotheses on the determinants of spatial patterns in savannas, and the role of herbivores.

In chapter 5 I analyse the effects of herbivores on the formation of patterns in savannas further, with a more mechanistic approach. This chapter addresses the second research question of this thesis. In this study we keep the total amount of forage removed by the herbivores constant, which is realistic for managed systems but not for natural systems. We focus on self facilitation and spatial dependence of grazing by herbivores. This helps us to understand under which conditions herbivores will be able to create permanent spatial heterogeneity in savannas.

Chapter 6 focuses on the consequences of dynamically responding herbivore populations on the dynamics and stability of the savanna system, which relates to the third research question in this thesis. We analyse the interactive effect of grazers and browsers on the stability of the savanna system, and the consequences of this interaction for the management of savanna ecosystems.

Chapter 7 investigates the spatial aspects of burning on savanna dynamics, and (as chapter 6) relates to the third research question of this thesis. Especially the effect of scale of burning is analysed and discussed. This is investigated in a spatially explicit simulation model. By analysing multiple realisations of the same model, we extract the general behaviour of the model. We specifically look for differences in catastrophic shift occurrence in the model, and how this occurrence, and the related resilience of the system is affected by the scale of the simulated fires.

Chapter 8 synthesises the findings from the previous chapters, and generalizes the models presented in chapters 4, 5, 6 and 7, by integrating the different aspects. Also, I discuss the implications of our findings for savanna management and what questions are still open.

CHAPTER 2

Correlations between tree patterns in African savannas and top-down and bottom-up factors: a continental analysis

THOMAS A. GROEN, FRANK VAN LANGEVELDE, CLAUDIUS A.D.M. VAN DE VIJVER, ANNELOES L. DE RAAD, JAN DE LEEUW & HERBERT H.T. PRINS

Abstract

This paper explores the possible correlations between spatial processes and tree grass patterns in savannas. Tree patterns on aerial photographs were quantified making use of landscape indices, including total cover, tree patch size, nearest neighbour distances and shape indices. They were correlated with factors that were expected to play a role in the origin or continuation of patterns. These factors were divided in factors that regulate tree growth bottom up, for example, through the availability of resources, and factors that control tree abundance top down through the removal of above ground biomass, for example, the consumption of foliage through herbivory by goats. We found that top-down factors correlated stronger with tree pattern indices than bottom up factors. However, significant relations found between mean annual precipitation and the 90% quantile of total tree cover and between human density and the 90% quantile of total tree cover suggested that some factors might play an important role in setting boundaries on which patterns are possible, while other factors determine within these boundaries the realised pattern. In all the regression analyses performed, the scale of the analysed aerial photographs appeared to play an important role as well, suggesting that a subsequent study with aerial photographs of only one scale could be worthwhile.

Keywords: *spatial pattern, nearest neighbour, abiotic conditions, precipitation.*

Introduction

The importance of spatial processes for ecosystem functioning has long been recognised in ecology (Tilman & Kareiva 1997, Wiens 1989). Especially the effect of spatial processes on spatial patterning and vice versa is an intriguing aspect that makes understanding ecosystems dynamics a complex issue (Wagner & Fortin 2005). For several systems it has been suggested that spatial processes generate spatial patterns (Lejeune *et al*. 2002, Rietkerk *et al*. 2002), and that these patterns contribute to the stability in the system (Ludwig *et al*. 1999, Van de Koppel & Rietkerk 2004). However, empirical evidence for the determinant of spatial patterns is often unavailable, because many processes interact and the scale is often too large for experiments. It is therefore difficult to disentangle the relative importance of the different processes on the spatial pattern and vice versa.

Insight in the processes that dominate the formation of spatial patterns can be of importance for the management of ecosystems. Some processes (*e.g.*, burning or herbivory by livestock) are easier to control by managers than others (*e.g.*, long spells of drought). Knowing in advance which processes are determining patterns is therefore important to set management priorities. This study addresses the question which processes are in control of patterns in savannas by investigating their correlations with patterns, and their relative importance in explaining variation in these patterns.

Finding a correlation between processes and patterns does not necessarily imply that the processes are causing the pattern. However, searching for existing relations between patterns and dominant spatial processes can reveal insights and help with the formulation of testable hypotheses.

We studied the correlations between tree patterns and factors of which we expect that they would interfere with these patterns in savannas. Savanna ecosystems consist of a continuous grass layer with a discontinuous tree layer (Scholes & Archer 1997). They occur over a wide range of climatic and edaphic conditions (Sankaran *et al*. 2005, Scholes & Archer 1997), both of which contribute to a high variety in tree cover between savanna ecosystems. Furthermore tree cover is determined by a variety of spatial processes like burning (Trollope 1984, Van de Vijver 1999, Van Langevelde *et al.* 2003), herbivory (Prins & Beekman 1989) and competition for resources (Ludwig *et al.* 2004). Savanna trees are easily recognized on aerial photographs because they contrast with grass dominated areas, and therefore we used these to quantify tree patterns.

We distinguish top-down and bottom-up factors that might correlate with savanna tree patterns. Top-down factors are factors that potentially reduce tree biomass, for example as a result of fire (Bond & Keeley 2005) or herbivory (Goheen *et al*. 2007). Bottom-up factors are factors that influence the growth of trees (Scholes & Archer 1997, Eamus *et al.* 1999).

Methods

Aerial photographs

To analyze tree patterns we used 128 aerial photographs covering 33 different areas in 17 countries throughout the African continent (Figure 2.1, Table 2.1). The scales of the photographs varied from 1:4,000 to 1:50,000 and were taken in the period from 1950 to 1988. All photographs were scanned with a resolution of 800 DPI. Due to different scales of the photographs, this resulted in pixels corresponding to 0.17 up to 2.12 m in reality. To standardize the data, all photographs were rescaled to pixel sizes of 0.15 m. Each selected aerial photograph was classified through visual interpretation into 'trees' and 'remaining land cover'. From each photograph we selected areas covered by a tree-grass mixture while excluding areas that contained rocky outcrops or steep slopes. The aerial photographs were

Table 2.1 Overview of the different areas with savanna vegetation for which aerial photographs were analysed.

Country	Area	Nr. photo’s of the area	Longitude				Latitude				Scale		Date
Botswana	Okavango Delta	3	23°	06’	51”	W	19°	23’	58”	S	1:	40,000	1973
Burkina Faso	Ouagadougou	4	1°	48’	00”	E	12°	12’	00”	N	1:	10,000	1988
Ethiopia	Didesa Wolega	6	35°	27’	00”	W	9°	33’	36”	N	1:	50,000	unknown
Gambia	Alicali	6	15°	43’	59”	E	13°	31’	59”	N	1:	20,000	1956
	Jowara	1	16°	04’	47”	E	13°	34’	36”	N	1:	20,000	unknown
	Kudang	4	15°	43’	59”	E	16°	40’	59”	N	1:	25,000	1980
Ghana	Ayensu River Basin	3	0°	28’	47”	E	6°	09’	00”	N	1:	12,600	1975
	Gambaga	2	0°	15’	36”	E	10°	19’	12”	N	1:	30,000	unknown
	Tamne River Basin	8	0°	41’	56”	E	10°	48’	21”	N	1:	30,000	unknown
Kenya	Athi River	2	37°	51’	00”	W	1°	51’	00”	S	1:	25,000	unknown
	North of Kapenguria	3	35°	04’	12”	W	1°	02’	25”	N	1:	20,000	1967
	Taita Hills	4	35°	15’	00”	W	3°	08’	59”	S	1:	10,000	unknown
Libya	Wadi Meginin	2	16°	27’	04”	W	30°	00’	00”	N	1:	24,000	unknown
Malawi	Machinga	2	35°	31’	00”	W	14°	58’	00”	S	1:	25,000	unknown
	Mzimba District	2	33°	20’	25”	W	11°	31’	11”	S	1:	25,000	unknown
	Ntcheu Hills Border Mozambique	1	34°	22’	48”	W	14°	29’	25”	S	1:	25,000	1976
Mali	Balle	2	8°	21’	00”	E	15°	12’	00”	N	1:	50,000	unknown
	Fina Forest	2	8°	18’	00”	E	12°	30’	00”	N	1:	50,000	unknown
	Sandare diema doubala	4	10°	10’	47”	E	14°	25’	11”	N	1:	50,000	1977
Morocco	Agadir	2	8°	33’	00”	E	30°	23’	59”	N	1:	7,500	unknown
Mozambique	Luabo sena Sugar estate	4	36°	06’	19”	W	18°	23’	34”	S	1:	20,000	1950
Nigeria	Bukkuyum	1	5°	28’	00”	W	12°	07’	59”	N	1:	40,000	unknown
	Eastern Zamtava	2	4°	01’	48”	W	12°	01’	47”	N	1:	40,000	unknown
	Gummi	1	5°	05’	23”	W	12°	05’	23”	N	1:	40,000	1962
South Africa	Nylsvly	16	28°	41’	42”	W	24°	36’	59”	S	1:	4,000	1974
Sudan	Penko Plain	4	30°	59’	52”	W	7°	12’	03”	N	1:	50,000	unknown
Tanzania	Babati District	5	35°	27’	00”	W	4°	07’	47”	S	1:	25,000	unknown
	Bagamoyo	7	38°	23’	59”	W	6°	15’	35”	S	1:	12,500	unknown
	Kahama	10	32°	30’	00”	W	3°	21’	00”	S	1:	40,000	1975
	Lake Manyara	2	36°	15’	00”	W	3°	18’	00”	S	1:	10,000	unknown
	Tarangire	12	36°	00’	00”	W	4°	00’	00”	S	1:	50,000	unknown
Tunisia	Djebel Fkirine	1	9°	52’	55”	E	35°	56’	20”	N	1:	25,000	unknown
Zimbabwe	Piriwiri	3	29°	28’	19”	E	19°	10’	24”	S	1:	25,000	1984

black and white images and classes were assigned using grey values as criterion. Because the contrast varied between the images, we distinguished three grades of quality for the classification (1=good, 2=reasonable and 3=bad). Figure 2.2 shows an example of these three quality classes.

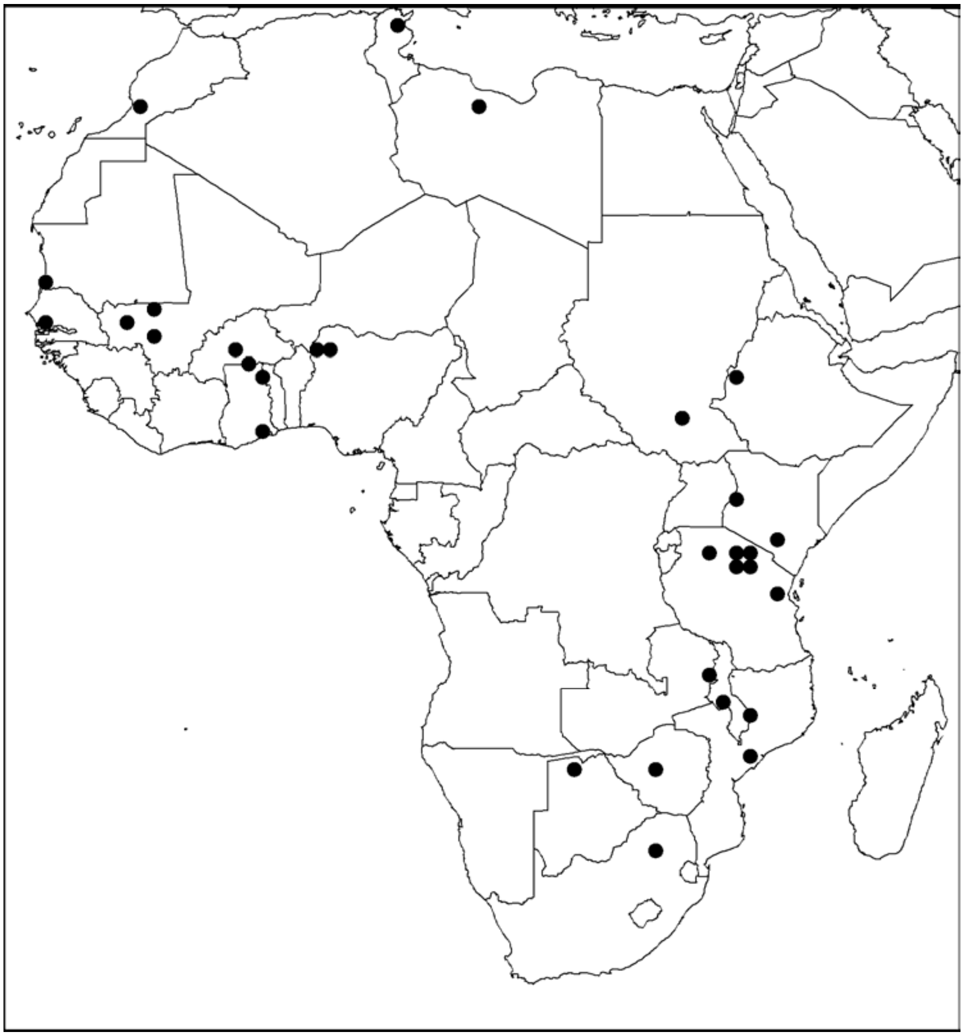


Figure 2.1 Locations of the different areas with savanna vegetation for which aerial photographs were obtained on the African continent.

The spatial extent of the photos varied. To standardize the extent over which tree pattern indices were collected, each photograph was subdivided in equal sized square partitions of 50 ha in which the tree patterning was measured using tree pattern indices (see below). These indices were averaged over the different partitions and, if available, over the different photographs in an area.

Quantifying tree patterns

Spatial tree patterns were quantified using landscape indices (Table 2.2, McGarigal & Marks 1993). These resulting tree pattern indices used in this study can be grouped in two different types: indices that relate to tree abundance and indices that relate to the shape of tree patches.

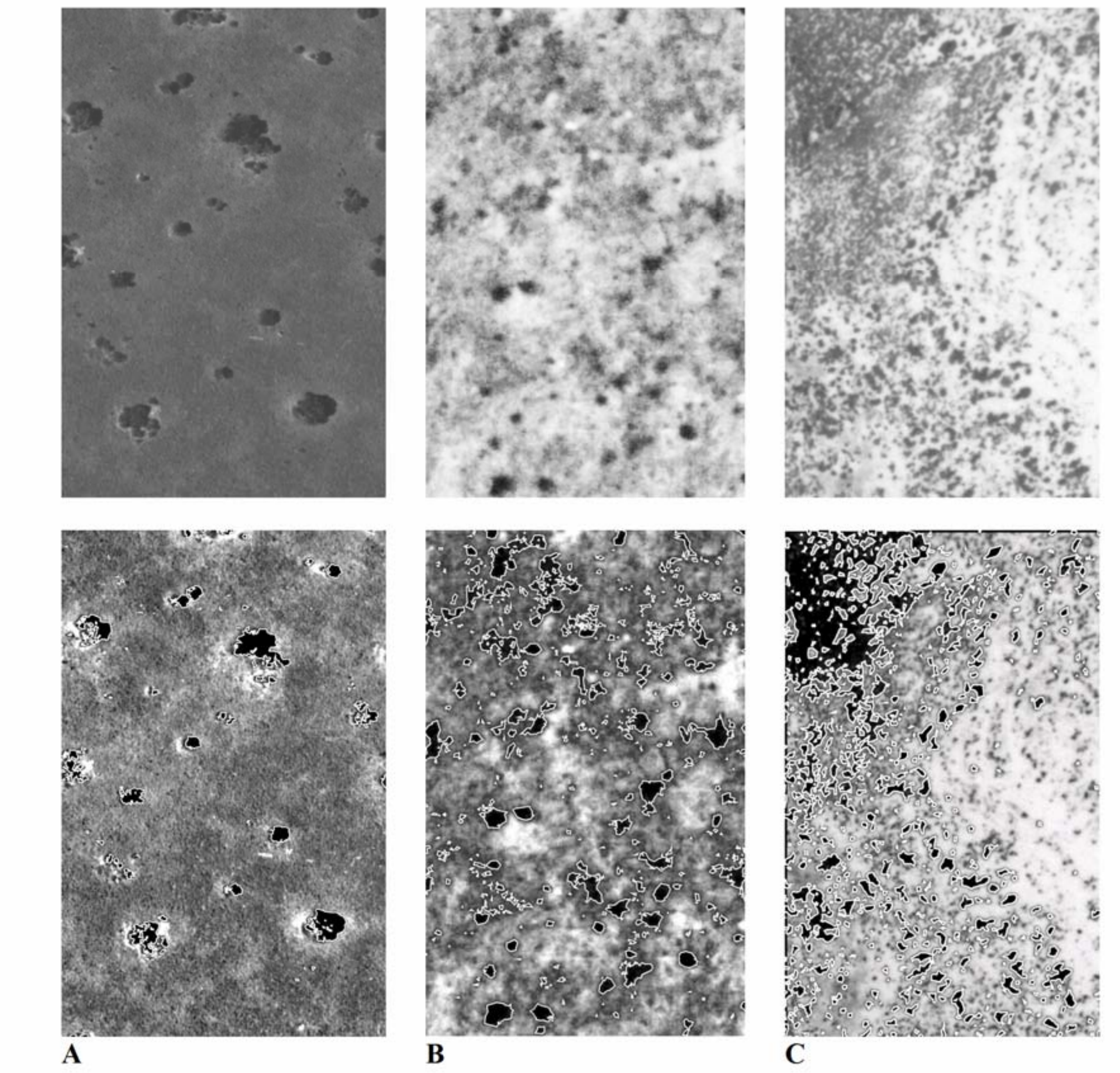


Figure 2.2 Example of a good (**A**; Nylsvlei, South Africa), reasonable (**B**; Alicali, the Gambia) and bad (**C**; Djebel Fkirine, Tunisia) photographs (upper photo's) and their classifications (lower photo's). White delineations indicate patches of trees. Good classifications had easily recognizable distinct edges between tree patches and other land use types (large contrast in grey pixels), for reasonable classifications the edge between tree and other land use types became more gradual (fuzzy), and with bad classifications the edge between tree patches and other land use types was even harder to distinguish.

Tree cover is a qualitative measure of the abundance of trees that can be easily measured, and which is included in many studies on trees in savannas (*e.g.*, Archer 1989, 1990, Brown & Carter 1998, Sankaran *et al.* 2005). Tree cover is related in these studies to several factors including grazing pressure and rainfall.

The number of tree patches per unit area is an indicator of the spatial arrangement of trees in the landscape, high numbers indicate tree scattering while low numbers indicate tree grouping. The spatial arrangement of trees is influenced among others by interspecific competition, dispersion and facilitation (Caylor *et al.* 2003, Jeltsch *et al.* 1996, Lejeune *et al.* 1999, Smith & Goodman 1986). An example of competition between trees could be the

Table 2.2 Description of the different tree pattern indices used in this study (McGarigal & Marks 1993). A is the area that a photograph of tree patch covers, N is the number of individual patches in an area, n is the distance of a patch to the nearest neighbouring patch and E is the length of the total patch perimeter.

Symbol	Name	Units	Range	Calculation
Tree abundance related pattern indices				
TC	Total tree cover	%	0 - 100	$\left(\sum_{i=1}^{N} A_i \Big/ A_{partition}\right) * 100\%$
PD	Tree patch density	# km^{-2}	0 - ∞	$N / A_{partition}$
MPS	Mean tree patch size	m^2	0 - ∞	$\sum_{i=1}^{N} A_i \Big/ N$
CVPS	Coefficient of variation of the mean tree patch size	m^2	0 - ∞	$\sqrt{\frac{\sum_{i=1}^{N} (MPS - A_i)^2}{N}} \Big/ MPS$
MNN	Mean nearest neighbour distance of patches	m	0 - size of partition	$\sum_{i=1}^{N} n_i \Big/ N$
CVNN	Coefficient of variation of the mean nearest neighbour distance of patches	m	0 - size of partition	$\sqrt{\frac{\sum_{i=1}^{N} (MNN - n_i)^2}{N}} \Big/ MNN$
Patch shape complexity related pattern indices				
ED	Density of tree patch edge	m km^{-2}	0 - ∞	$\sum_{i=1}^{N} E_i \Big/ A_{partition}$
MPSI	Mean patch shape index	m m^{-2}	0 - ∞	$\left(\sum_{i=1}^{N} \frac{0.25E_i}{\sqrt{A_i}}\right) \Big/ N$
MASI	Mean area shape index	m m^{-2}	0 - ∞	TC/ED
MPFD	Mean patch fractal dimension	-	1 - 2	$\left(\sum_{i=1}^{N} \frac{2\ln(0.25E_i)}{\ln(A_i)}\right) \Big/ N$

interference of root systems for the uptake of water or nutrients (Lejeune *et al.* 1999), and an example of facilitation between trees could be for example protection of each other from fire (Jeltsch *et al.* 1996, Chapter 3). In case of competition, trees are better-off far away from each other, and an over dispersed pattern (*i.e.*, long distances between trees) is expected, while in case of facilitation trees are better-off close to each other, and a clustered pattern is expected. If neither competition nor facilitation is important or equally strong, trees would be expected to occur in a random spatial arrangement.

Mean tree patch size and the coefficient of variation (C.V.) of this mean both give an indication of the spatial arrangement of the trees. Large patches can only grow when facilitation, limited dispersion, or both outweigh the process of competition. Otherwise, smaller (single tree) patches are more likely to occur. Low C.V. values of mean tree patch size can be the result of structuring processes. For example, high fire frequencies may result in the survival of large tree patches only, leading to a lower C.V. (only large tree patches present), while at low fire frequencies C.V. is expected to be higher (both large and small tree patches present).

Edge density, mean patch shape and mean patch fractal dimension (see Table 2.2) are indices that give an indication of the shape of tree patches (McGarigal & Marks 1993). We expect that these indices should especially be correlated with processes that operate at the edge of trees and grasses. For example grass fires will mostly damage trees at the edge of tree patches reducing possible irregular shapes in tree clusters, thus “eroding” shapes into more compact round forms.

Mean nearest neighbour distances between clusters and the C.V. of the mean of these nearest neighbour distances indicate how tree clusters are organised in the area. When low resource availability leads to severe competition, for example, a correlation between nearest neighbour distances and nutrient availability can be expected (Couteron & Lejeune 2001, Lejeune *et al.* 1999).

Explaining factors

We used 12 explaining factors, which are listed in Table 2.3. These factors were grouped into three categories: top-down factors, bottom-up factors and factors indicating the quality of the tree cover data. Factors are classified as top-down factors when they regulate tree growth through removal of biomass. We included the following top-down factors: mean fire return interval and its C.V. of the mean fire return interval, sheep and goat densities (combined into one factor) and cattle densities. Since these factors can be controlled to some extent by people, we also included human population density. Bottom-up factors control tree growth, and are often outside control of people and relate to the climate or topography of the location of the pattern. The following bottom-up factors were included: mean annual precipitation, maximum mean monthly temperature, the number of growing days, total exchangeable bases in the top 30 cm of the soil, and soil depth. Initially monthly minimum precipitation and yearly average and monthly minimum temperatures had been included, but were subsequently omitted because they showed strong co linearity with precipitation and maximum temperature respectively. The last explaining category reflects the quality of the different data sources and contains the quality class of each photo (see previous section) and the scale of the photo. We expect that small scale photos (1:50,000) do not represent tree cover and patch shape as accurately as large scale ones (1:4,000). We thus assume that large scale photos had better quality.

Statistical analysis

The two datasets with (i) tree pattern indices and (ii) the explaining factors were first analysed on possible correlations within the datasets using principal component analysis (PCA, Van der Brink & Ter Braak 1998). Then, prior to the analysis of the correlation between the tree pattern indices and the explaining factors, we hypothesized the direction of these correlations (Table 2.4). Top-down factors were expected to be negatively correlated with most tree pattern indices, because these factors are expected to contribute to removal of tree biomass, though, mean nearest neighbour distances are expected to correlate positively with top-down factors. When tree patches are suppressed and become scarce, their inter tree distances should increase. We also expected a positive correlation of mean fire interval with tree pattern indices, because an increase in mean fire interval means less fire, and therefore less suppression of trees. Lastly, although we included the C.V. of the mean fire interval in the analysis, we had no expectations on its effects on tree pattern indices.

The bottom-up factors, except maximum monthly temperature, were expected to be positively correlated with tree pattern indices. We expect that maximum monthly temperature correlates negatively with tree pattern indices because increased temperatures increase evapotranspiration, which leading to resource limitations, in contrast with the other bottom-up factors.

Table 2.3 Description of the human and environmental factors that are used in this study to explain tree patterns in savanna vegetation.

Symbol	Description	Range	Units	Source
		Top-down factors		
CATTLE	Cattle densities			FAO
SHOAT	Sheep and goat density combined			FAO
MFIRINT	Mean interval between fires	21 - 311	wk	Barbosa *et al.* 1999
CVFIRINT	Coefficient of variation of the mean interval between fires	0 - 1.7	wk	Barbosa *et al.* 1999
HUMDEN	Human population density	7 - 235	people km^{-2}	LandScan 2005
		Bottom-up factors		
GRODAY	Nr. of grow days	4 - 11	d	FAO
TMAX	Maximum mean monthly temperature	21 - 36	$^{\circ}$C	FAO
PREC	Precipitation	254 - 1272	mm	Falling Rain 2006
TEBT	Total exchangeable bases in the top soil	1.7 - 32.7	cmol$_C$ kg^{-1}	Batjes 2005
DEPTH	Soil depth	0 - 190	m	Batjes 2005
		Quality factors		
SCALE	Scale of the original aerial photograph	1:4.000 - 1:50.000	-	-
GRADE	The quality of the classification (see Figure 2.2 for examples)	1 - 3	-	-

We used regression and quantile regression (Koenker & Basset 1978, Koenker 2006) to analyse the correlation between the explaining factors and the tree pattern indices. Only the main effects of the explaining factors on the tree pattern indices were tested. Interactions between the explaining variables were not considered because of restrictions imposed by the limited sample size. To investigate correlations between explaining factors and the tree pattern indices, we started by formulating for each tree pattern index a regression model for every possible combination of explaining factors as predictors. This yielded for each tree pattern index 2^{12}=4096 possible models. We estimated all of these models and selected the best model based on its Akaikes information criterion (AIC, Quinn & Keough 2002). AIC is a measure of the goodness of fit of a statistical model and gives a penalty for including more parameters to avoid over fitting. Lower AIC values indicate better fits. We tested the significance of the model with the lowest AIC value.

Second, we performed quantile regression (Koenker & Basset 1978) on those relations that promised to be interesting at first glance on scatter plots with the top-down and bottom-up factors on the x-axis and the tree pattern index on the y-axis, as well as on the same relations that have been investigated by Sankaran *et al.* (2005). Sankaran *et al.* found that although rainfall does not necessarily predict actual tree cover, it sets an upper bound on tree cover once annual rainfall drops below ± 650 mm. For quantile regression we used the quantreg package for the R statistical program (Koenker 2003). We report only on significant relationships.

Following the regression analyses, we investigated which type of factor (top-down of bottom-up) had a stronger effect on tree pattern indices, making use of hierarchical partitioning and model selection based on AIC. We used two different statistical approaches to investigate the strength of the found the correlations with top-down and bottom-up factors between both approaches. For the first approach we calculated the independent R^2 — expressed as percentage of the total R^2 of a model including all factors — of each top-down and bottom-up factor on each tree pattern index using hierarchical partitioning (Chevan & Sutherland 1991, Quinn & Keough 2002). We call this the hierarchical partitioning approach. The basic idea behind hierarchical partitioning is to calculate the part of the explaining power of a predictor that is not "shared" by other predictors. In other words, the independent R^2 is the percentage variance explained by a predictor, which can not be explained by any other predictor in the dataset. To calculate the independent R^2 of a predictor, all possible multiple regression models with and without that predictor are calculated. Then, the differences between the R^2 of the full and reduced models for each parameter are calculated. Accordingly, the average of this difference in R^2 is first calculated at each hierarchical level (so for each model with 1, 2, 3,… *etc.* predictors), and then over the different hierarchical levels. We used the package hier.part in R (Walsh 2004) to calculate the independent R^2.

As a second approach, we selected the best 200 models for each tree pattern index, based on their AIC, and scored how many times a factor was included in these models. We call this the AIC approach.

Both approaches yielded an indication of how important an explaining factor is, compared to the other factors. We then compared the scores of the top-down and bottom-up factors by summing up their AIC-scores or independent R^2 values. We compared the sum of scores between top-down and bottom-up factors for all tree pattern indices for both methods.

Because we were dealing with a limited number of observations, and because variation was large we decided to accept 0.1 as a critical level for significance. However, to enable the reader to form their opinion, we included P values where possible, either as exact values or as classes.

Results

Figure 2.3 shows the PCA ordination diagrams for the tree pattern indices and the explaining factors. The tree pattern indices show a distinct division of groups (Figure 2.3A). Mean nearest neighbour distances deviated, correlating negatively with the other tree pattern indices. This is further illustrated in Figure 2.4 where correlations between tree cover and the other tree pattern indices are shown. Tree cover correlates strongly with all tree pattern indices except for patch density, mean patch fractal dimension and the C.V. of nearest neighbour distances. Only mean nearest neighbour distances correlate negatively with tree cover.

The explaining factors show more dispersal within the biplot (Figure 2.3B), but some pattern emerges. Abundance of sheep and goats, the abundance of cattle, and mean fire return interval correlate positively to each other, but negatively with the C.V. of the mean fire return interval. Human density and mean annual precipitation appear positively correlated but negatively correlated with other climate factors (maximum monthly temperature and number of growing days) and total exchangeable bases in the topsoil.

Table 2.4 The expected correlations between tree pattern indices and top-down and bottom-up factors (+ = positive correlation, - = negative correlation, ? = none expected). Between brackets the correlations as determined by the lowest Akaikes Information Criterion (AIC). The P value and R^2 and R^2 adjusted in the table give the values for the over-all model, symbols in the table indicate the significance levels for each bottom-up and top-down factor.
Significance: * 0.05 < P < 0.1, ** 0.01 < P < 0.05, *** P < 0.01

				Top-down factors					Bottom-up factors					Quality factors	
Tree Pattern Index	P-Value	R^2	R^2 Adjusted	CATTLE	SHOAT	MFIRINT	CVFIRINT	HUMDEN	GRODAY	TMAX	PREC	TEBT	DEPTH	GRADE	SCALE
Tree abundance related pattern indices															
TC	0.085	0.11	0.08	-	-	+	?	-	+	-	+	+	+	?	?(-*)
PD	0.005	0.35	0.30	-	-	+	?	-	+	-	+	+	+	?(-**)	?(-
MPS	0.090	0.19	0.12	-	-	+(+**)	?	-(-)	+	-	+	+	+	?	?
CVP	0.037	0.24	0.17	-	-(-*)	+	?	-	+	-	+	+	+	?	?(-**)
MN	0.015	0.48	0.36	-	+	-	?	+	-	+(+)	-	-	-	?(-)	?
CVN	0.001	0.73	0.61	-	-	+(+***	?(+**)	-(-*)	+	-(+**)	+	+(+*	+(+**	?(-)	?(-)
Patch shape complexity related pattern indices															
ED	0.032	0.31	0.22	-	-(-*)	+	?	-	+	-	+	+	+	?(-*)	?(-**)
MPS	0.280	0.05	0.01	-	-	+	?	-	+	-	+	+	+	?	?
MAS	0.220	0.06	0.02	-	-	+	?	-(-)	+	-	+	+	+	?	?
MPF	0.000	0.77	0.74	-	-(-***)	+	?	-	+	-	+	+	+	?(+)	?(-

Table 2.4 shows the prior defined expected direction of correlations between tree pattern indices and explaining factors, and (between brackets and in bold) the observed correlations based on models with the lowest AIC. For these models, the direction of all observed correlations correspond with the a-priori formulated directions except for the correlation between maximum monthly temperature and the C.V. of the mean nearest neighbour distances, precipitation and total exchangeable bases in the soil and mean nearest neighbour distances. Most models found were significant at the 5% level, except for total tree cover and mean patch size which were significant at the 10% level and for mean patch shape index and mean area shape index which were not significant at the 10% level. Also a regression on the 90% quantile for mean annual precipitation and total tree cover and for human density and total tree cover (Figure 2.5) yielded significant models. The relation between mean annual precipitation and total tree cover was based a subset of the data with precipitation less than 650 mm, following the analyses as performed by Sankaran *et al.* (2005).

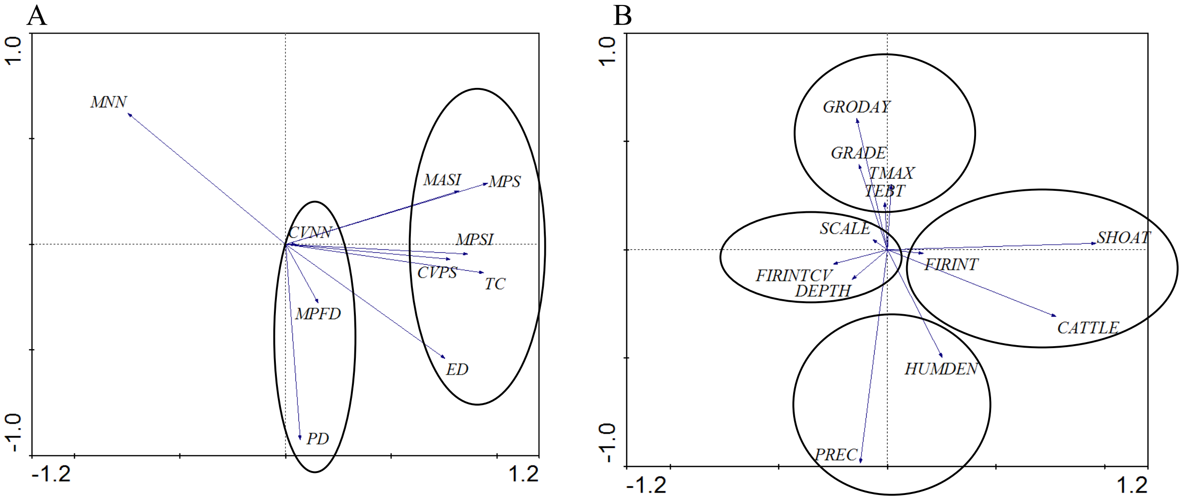


Figure 2.3 The results of the principal component analysis on (A) the tree pattern indices and (B) the explaining factors plotted along the first (x-axis) and second (y-axis) principal components. Circles indicate a rough grouping of indices. Abbreviations are explained in Table 2.2 and 2.3.

Table 2.5 shows the scores for the AIC approach and the hierarchical partitioning approach for the different explaining factors and tree pattern indices. We also calculated the total scores for the top-down factors, bottom-up factors and quality factors. Because we have an equal number of top-down and bottom-up factors, we can compare these factors directly. For tree pattern indices related to tree abundance, most top-down factors have higher scores than the bottom-up factors. The only exceptions were total tree cover, mean nearest neighbour distances and the C.V. of the nearest neighbour distances for the hierarchical partitioning approach, and mean nearest neighbour distance and coefficient of the mean of the nearest neighbour distances for the AIC approach. For patch shape complexity related tree pattern indices both approaches yield opposite results. For the hierarchical partitioning approach, the scores for top-down factors are lower than the bottom-up factor scores, except for the mean patch fractal dimensions. For the AIC approach the scores are higher for the top-down factors than for the bottom-up factors.

In our analyses we corrected for the quality of the data. This proved to be an important step because both the variables SCALE and GRADE were included in many models selected on AIC (Table 2.4), and obtained very high scores both in the hierarchical partitioning approach and the AIC approach. By including SCALE and GRADE, and taking account of their effects, we are able to focus our attention on the factors that are of interest.

Table 2.5 The partial R^2 values and the AIC scores for the bottom-up and top-down factors for the different tree pattern indices.

	Tree abundance related landscape indices						Patch shape complexity related landscape indices			
	Hierarchical partitioning approach (%)									
	Top-down									
	TC	PD	MPS	CVPS	MNN	CVNN	ED	MPSI	MASI	MPFD
CATTLE	4.29	5.31	5.91	8.93	3.33	4.10	2.62	9.93	7.56	8.48
SHOAT	10.59	4.80	9.46	15.01	6.07	3.87	9.75	8.46	8.91	6.4
FIRINT	6.11	4.62	15.85	7.45	6.30	22.44	4.71	7.85	6.91	9.48
FIRINTCV	5.13	4.86	10.14	5.21	4.04	9.58	3.81	5.43	7.08	7.41
HUMDEN	4.66	10.10	7.47	5.05	4.96	7.22	3.04	4.56	11.14	4.74
Total top-down	30.79	29.68	48.83	41.65	24.69	47.20	23.94	36.22	41.59	36.56
	Bottom-up									
	TC	PD	MPS	CVPS	MNN	CVNN	ED	MPSI	MASI	MPFD
GRODAY	5.89	4.29	7.10	5.33	13.37	5.69	6.35	4.62	6.57	4.42
TMAX	11.55	4.72	12.95	7.86	4.86	4.98	3.69	11.84	11.95	4.76
PREC	4.97	6.27	4.98	4.57	12.96	7.28	3.53	5.70	7.40	3.71
TEBT	13.65	7.93	9.75	5.93	20.58	16.62	15.79	14.59	7.60	4.04
DEPTH	7.6	3.57	5.91	9.02	4.29	9.22	3.34	5.98	10.20	3.18
Total bottom-up	43.65	26.79	10.69	32.71	56.07	43.78	32.69	42.73	43.72	20.12
	Quality									
	TC	PD	MPS	CVPS	MNN	CVNN	ED	MPSI	MASI	MPFD
GRADE	4.86	13.57	5.07	6.71	5.57	5.26	8.47	5.04	8.10	7.93
SCALE	20.70	29.96	5.41	18.93	13.67	3.76	34.90	16.00	6.59	35.39
Total quality	25.56	43.53	10.48	25.64	19.24	9.01	43.37	21.04	14.69	43.32
	AIC approach (#)									
	Top-down									
	TC	PD	MPS	CVPS	MNN	CVNN	ED	MPSI	MASI	MPFD
CATTLE	42	47	40	43	44	76	59	72	35	53
SHOAT	71	79	46	128	90	79	129	52	31	200
FIRINT	38	68	147	56	66	200	39	39	42	48
FIRINTCV	48	63	49	53	41	160	80	40	30	46
HUMDEN	81	64	101	90	43	78	36	49	123	424
Total top-down	280	321	383	370	284	593	343	252	261	
	Bottom-up									
	TC	PD	MPS	CVPS	MNN	CVNN	ED	MPSI	MASI	MPFD
GRODAY	33	45	31	31	48	74	52	26	63	79
TMAX	55	46	56	40	105	149	28	42	61	38
PREC	27	52	49	36	186	100	44	29	34	46
TEBT	57	63	55	29	198	200	47	55	29	64
DEPTH	31	45	35	46	40	199	30	26	46	59
Total bottom-up	203	251	226	182	577	722	201	178	233	286
	Quality									
	TC	PD	MPS	CVPS	MNN	CVNN	ED	MPSI	MASI	MPFD
GRADE	31	197	26	31	107	108	122	29	31	91
SCALE	164	200	28	178	54	90	197	86	58	200
Total quality	195	397	54	209	161	198	319	115	89	291

Discussion

Our analysis suggests that top-down factors are more important in determining tree pattern indices that are abundance related than bottom-up factors. These factors can be easier controlled by people that the bottom-up factors, of which only mean annual precipitation and total exchangeable bases in the top-soil can be partly mediated through irrigation and fertilisation activities. These, however, are unlikely to happen in savannas. Our results thus suggest that for savanna structure, human influence can be considered a prime determinant. This in itself is not a surprising finding since it is widely acknowledged that human activities influence the savanna ecosystem already for millennia (Scholes & Archer 1997). However, this study quantifies the impact of these anthropogenic pressures. Also, we were able to distinguish the effect of separate factors that play a role in tree abundance of savannas. Only few of these correlations were significant, but all significant correlations for the top-down factors on tree abundance related factors concurred with a-priori formulated hypotheses. Thus, the density of sheep and goats had a negative correlation with the C.V. of the mean patch sizes, suggesting that with increasing browsing pressure the variation in patch sizes diminishes. Mean fire interval had a positive correlation with both mean patch size and the C.V. of the mean nearest

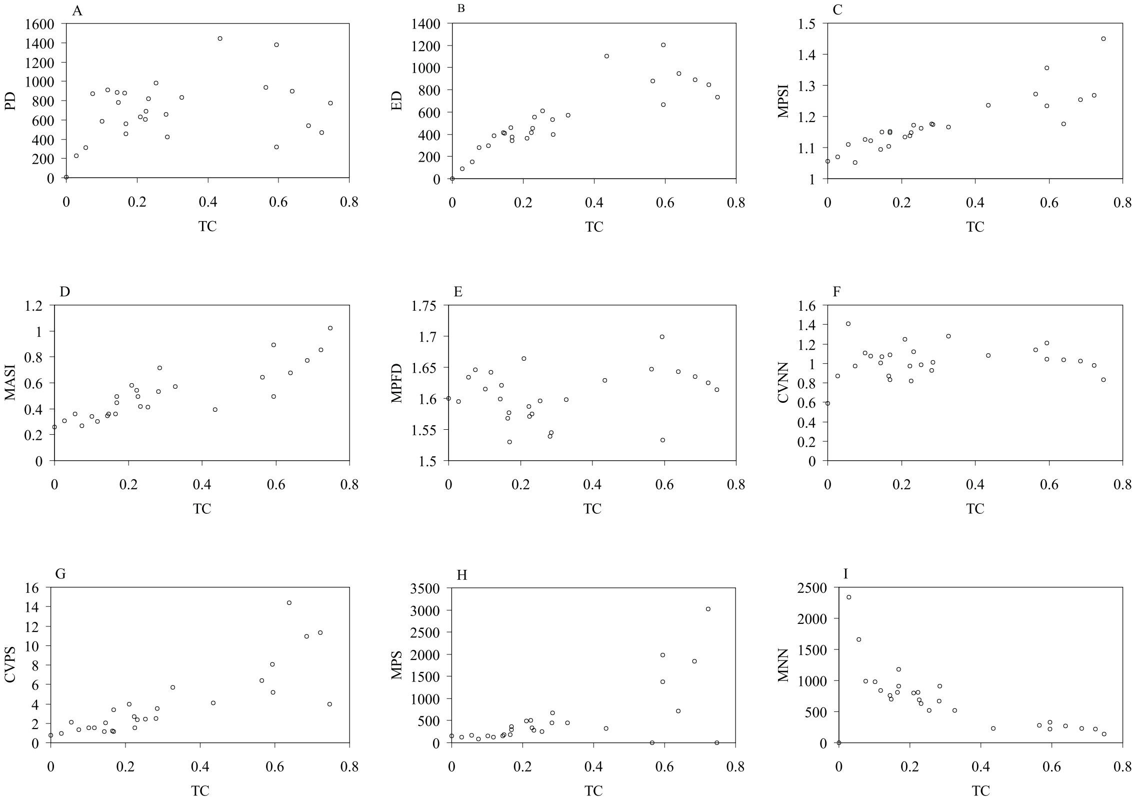


Figure 2.4 Correlations between total cover and (A) patch density (R2=0.03, P=0.411), (B) edge density (R2=0.76, P<0.001), (C) mean patch shape index (R2=0.73, P<0.001), (D) mean area shape index (R2=0.66, P<0.001), (E) mean patch fractal dimension (R2=0.04, P=0.376), (F) coefficient of variation of the mean nearest neighbour distances (R2=0.002, P=0.826), (G) coefficient of variation of the mean patch size (R2=0.80, P<0.001), (H) mean patch size (R2=0.73, P<0.001, and (I) mean nearest neighbour distances (R2=0.58, P<0.001). Abbreviations as in Table 2.2 and 2.3.

neighbour distances, showing that with increasing fire intervals, patches have a chance to grow larger and that variation in inter patch distances increases as well. Also the C.V. of the fire interval correlates positively with the C.V. of nearest neighbour distances. Human density had a negative effect on the C.V. of the mean nearest neighbour distances. We also found through quantile regression that human density has a negative correlation with total tree cover. These observations suggest that with increasing human density tree cover declines. Also, the other top-down factors have a negative correlation with total tree cover, or related tree pattern indices. This suggests that human activities (*e.g.*, fire and livestock) in savannas indeed keep the savanna biome open.

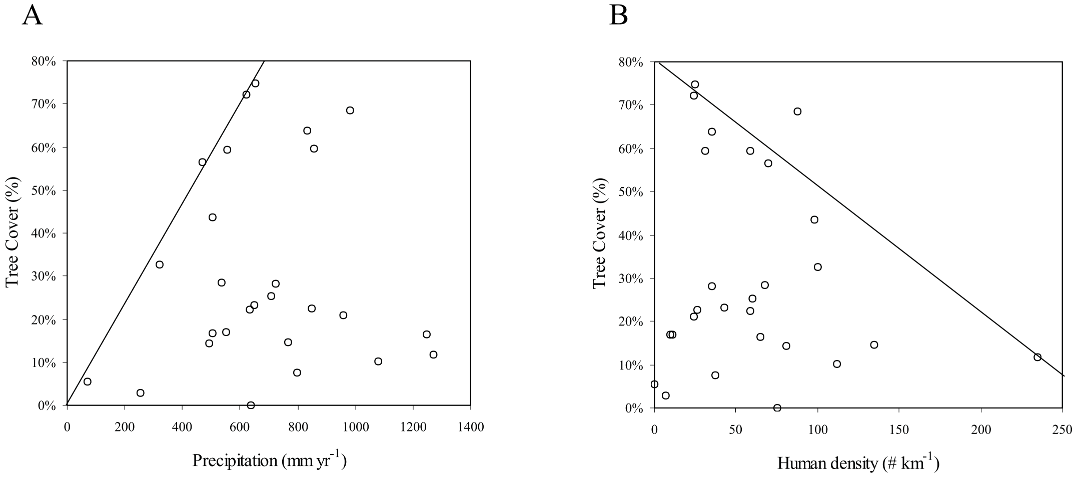


Figure 2.5 The found significant relationships for the 90% quantile between (A) precipitation (PREC) and total tree cover (TC) with precipitation below 650 mm and (B) human density (HUMDEN) and total tree cover (TC). For precipitation and total tree cover the relation is TC=0.12*PREC-2.77 and for human density and total tree cover TC=-0.29*HUMDEN+79.10.

Sankaran *et al.* (2005) investigated the effects of a number of factors on tree cover in savannas, including mean annual precipitation, fire return interval, present herbivore biomass, several soil characteristics. With an impressive dataset of 854 sites they had difficulties establishing significant relationships between tree cover and these factors. However, they found an interesting relationship for precipitation and tree cover using quantile regression. In their study, maximum tree cover was found to be positively correlated with mean annual precipitation up to 650 mm per year, above which cover seemed not to increase any more. We performed a similar regression on our much smaller dataset, including only sites with precipitation less than 650 mm. We found a very similar significant slope for the regression of 0.12 (% tree cover per mm of mean annual precipitation) compared to a slope of 0.14 found by Sankaran *et al.* (2005), which shows that although we find that top-down factors correlate better with tree patterns, bottom-up factors like rainfall still play a very important role by setting the upper bounds of what is attainable in a savanna.

A result that urges for continuation of this explorative study is that our quality factors (SCALE and GRADE) turned out to be very important in explaining variation between found patterns. Future studies therefore should take note of this important effect and try to avoid collecting data at different spatial scales. With the continuation of ever-improving remote sensing products and its dissemination through new channels, like for example Google Earth, the possibility of repeating the study with a larger and qualitatively better dataset is becoming an option that is not far from reality anymore. However, in previous studies with large data sets

(Sankaran *et al.* 2005), it proved that variation among sites will be large, and that detecting trends for savanna pattern are difficult.

In this study we investigated the correlations between several factors and tree patterns in African savannas. We showed that top-down factors correlate better with pattern indices that relate to tree abundance, but that bottom-up factors can play an important role because they set the boundaries, like in our and other studies mean annual precipitation.

Acknowledgements

We would like to thank Benno Masselink for his assistance during the collection of the aerial photography, Paul Loth for helping with collecting photography from Lake Manyara NP and Frans Rip for helping with the technical aspects of classifying the photography. Gerrit Gort willingly discussed various statistical techniques with us. Paul Loth gave useful comments that improved the manuscript.

CHAPTER 3

Clustering of savanna trees reduces damaging effects of fire in South African Savannas

THOMAS A. GROEN, FRANK VAN LANGEVELDE, CLAUDIUS A.D.M. VAN DE VIJVER, NAVASHNI GOVENDER & HERBERT H.T. PRINS

Abstract

In this paper, we investigate two possible mechanisms that can lead to clustering of trees in savanna ecosystems: (1) protection against fire (defined as a “passive process”); and (2) seedling establishment (defined as an “active process”). This was tested by measuring clustering of trees using the T-squared sampling method in plots of the Kruger National Park experimental burning program. Next to the fire return interval, we used several auxiliary determining parameters like clay content in the soil, diameter of tree canopies, understorey composition, tree species diversity and average annual rainfall. The data contained a lot of variation, but indicated that clustering is mostly an “active process” where tree seedling establishment close to mature trees is the determining factor. Fire frequency was also found to have an effect on clustering. By analysing the relationship between the distance of a tree to its nearest neighbour and its canopy diameter, we tested the effect of clustering on the impact of fire on trees. We found that although fire only weakly determines the clustering of trees, clustering reduces the damaging effect of fire on trees.

Keywords: *Africa, fire frequency, regression, spatial pattern, savanna ecology, tree clustering.*

Introduction

Spatial processes are increasingly gaining attention in ecology (Van Nes & Scheffer 2005), because they can create spatial patterns (Rietkerk *et al.* 2004), which can have an effect on ecosystem functioning (Rietkerk *et al.* 2002). A thorough understanding of key spatial processes as well as the effects of these processes on ecosystems is essential for developing predictive theory on patterns in ecosystems. Especially in spatially heterogeneous ecosystems, spatial processes are expected to play a key role (Van Nes & Scheffer 2005). Savannas are typically spatially heterogeneous because the ratio and spatial distribution of the main vegetation constituents, a continuous grass layer and a discontinuous tree layer, vary considerably (Scholes & Archer 1997).

In savannas, herbivory, fire and water availability play important roles in the dynamics and structure of the system (Scholes & Archer 1997, Van Langevelde *et al.* 2003). Herbivory and fire are typically spatial processes, as their impact on ecosystems largely varies in the landscape. The level of herbivory is mostly determined by the availability and accessibility of digestible plant material (Marion *et al.* 2004), while fire frequency and severity are determined by the local occurrence of ignition events, the fuel load (mostly grass in the case of savannas, Shea *et al.* 1996) and the possibility of the fire spreading to neighbouring areas (Berjak & Hearne 2002).

Modelling studies suggest that, apart from affecting tree density and cover, fire affects the spatial patterning of trees in savannas (Gignoux *et al.* 1998, Jeltsch *et al.* 1996, 1998). More specifically, a high fire occurrence is expected to increase clustering among trees (Gignoux *et al.* 1995, Jeltsch *et al.* 1996), because clustered trees are less affected by fire through their combined suppressing effect on grass biomass, and thus fuel load, than evenly spaced trees. However, little empirical evidence is available to support this hypothesis (Kennedy & Potgieter 2003).

An alternative mechanism that can induce clustering of plants is the combination of dispersal (seeds or clonal growth) and competition (*e.g.*, Pacala & Levin 1997). Due to limited dispersion ranges, seeds occur in higher densities near mother plants than further away, while plants nearby compete more strongly with each other than plants further apart. Clustering of plants is hypothesized to be a function of settlement of seedlings, while random patterns are caused by mortality of plants through, for example, herbivory or drought. Eventually, competition can lead to spacing out of plants, creating over-dispersed patterns.

In this paper, we investigate if these two mechanisms determine tree clustering in savannas, and how strong their effect is. If seedling establishment is an important mechanism in determining the clustering of trees, we would expect most trees in a cluster to be of the same species, and, therefore, the nearest neighbours of trees to be on average the same species as well. We define this as “active clustering”. If fire is an important mechanism determining clustering of trees, we would expect an increase in clustering with increasing fire occurrence as trees standing in clusters are better protected against fire damage than trees in an unprotected isolated location. We define this as “passive clustering”. If this mechanism operates in a savanna we expect that the nearest neighbours of trees can be of any species, including the same species.

Given the same density, clustered trees have shorter nearest neighbour distances than trees that are randomly or evenly spaced. The distance to nearest neighbours has an effect on the competition between individuals (Carrick 2003, Pacala & Levin 1997). Competition can reduce plant growth, with adverse implications for plant size, like canopy diameter. This means that trees that are close to each other may have smaller canopy diameters than trees further away. Plotting the distance of trees to their nearest neighbouring tree against their canopy diameters can give an indication of the strength of this competition (Smith & Goodman 1986). A positive, steep trend would suggest that competition between these trees affects their performance (Figure 3.1). Fire can also reduce the height of small trees, while its impact on larger trees is minimal (De Ronde *et al.* 2004). Because of a strong correlation between tree height and canopy diameter, the canopy diameter of savanna trees can be expected to be smaller with fire than without fire (Figure 3.1). The difference in canopy diameter between "with fires" and "without fire" indicates the impact of fire on trees. If larger trees experience a less negative effect from fire than smaller trees, their canopy diameter is hardly affected by fire (compare X1 with X2 in Figure 3.1A). However, if trees in clusters are better protected from fire than solitary trees, we expect that trees closer together experience a smaller negative impact from fire than trees that are further apart (compare X1 with X2 in Figure 3.1B). When the effect of fire on trees is not influenced by the height of trees or the distance to nearest neighbours, or when these two processes are equally strong in modifying the effect of fire and compensate each other, the effect of fire should be equally large at short nearest neighbour distances as well as long nearest neighbour distances (compare X1 with X2 in Figure 3.1C).

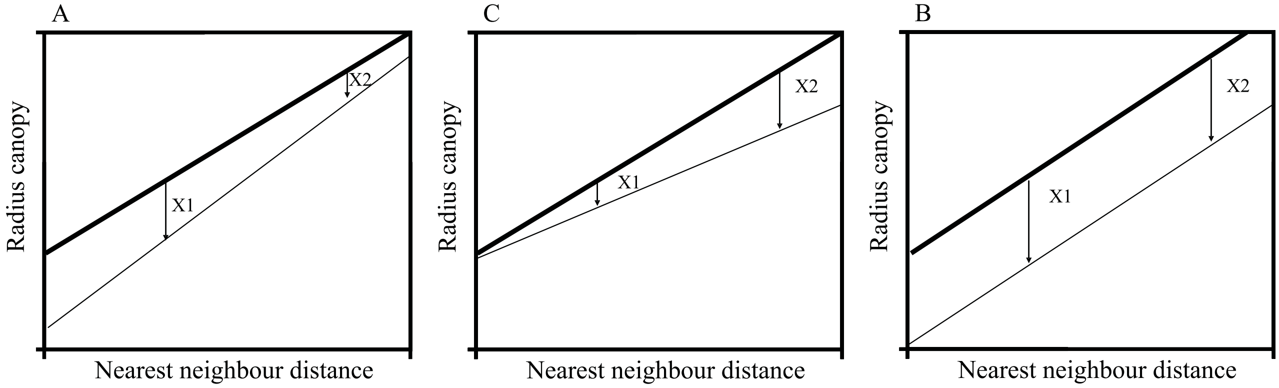


Figure 3.1 Hypothetical relationships between nearest neighbour distances and canopy diameters, and the effect of fire. Bold lines represent the potential positive relationship between nearest neighbour distances and canopy diameters if no burning takes place. Thin lines represent the potential positive relationship if burning does take place. (A) If large trees experience a less negative effect from fire than small trees, canopy diameter is hardly affected by fire (compare X1 with X2). (B) If trees in clusters are better protected from fire than solitary trees, we expect that trees closer together experience a smaller negative impact from fire than trees that are further away from each other. (C) When the effect of fire on canopy diameter of trees is not influenced by the height of trees or distance to nearest neighbours, or when these two processes are equally strong and compensate each other, the effect of fire should be equally large at short nearest neighbour distances as well as long nearest neighbour distances.

To investigate the degree to which fire and (lack of) seed dispersal (which is directly correlated with seedling establishment) contribute to tree clustering in savannas, we conducted a field study where we measured the clustering of savanna trees over a range of fire frequencies, and tested which environmental variables most determine clustering. We have two hypotheses to explain tree clustering: (1) protection against fire damage acts as a clustering mechanism (*i.e.*, "passive clustering"), and additionally (2) seedling establishment is an important clustering mechanism (*i.e.*, "active clustering"). If the first hypothesis is true we expect fire frequency to be positively correlated with clustering of trees. If the second hypothesis is true we expect that clusters will consist of same species. By analysing the relationship between the distance of a tree to its nearest neighbour and its canopy diameter, we also tested the effect of clustering on the impact of fire on canopy diameter as formulated in Figure 3.1.

Methods

Study site

The study was performed in the experimental burning program of the Kruger National Park in South Africa (Biggs *et al.* 2003). The program was initiated in 1954 and consists of 7-10 ha plots that are burned at varying intervals ranging from total fire exclusion to annual fires. Each treatment is repeated in all four major landscape types of the park (Gertenbach 1983). The major landscape types are roughly positioned in a north-south gradient (Figure 3.2), which coincides with a dry-wet rainfall gradient. The long-term average annual rainfall is 496 mm at Mopane in the north and 746 mm at Pretoriuskop in the south (KNP Scientific Services 2005; Table 3.1). Each burning treatment in each landscape type is replicated four times. For this study, the annual, tri-annual and no fire (control) treatments in each landscape type were used as study plots. This yielded a total of 48 different plots divided over three treatments, four landscapes and four replications.

Table 3.1 Average of predictor variables, separated per landscape and burn treatment.

Landscape	Intended fire frequency (1/yr)	Realized fire frequency (1/yr)	Plot fire intensity (kJ/m/s)	Precipitation (mm)	Distance to nearest water point (m)	Fuel moisture content (mass %)
Pretoriuskop	1.0	0.91	2429	746	1512.4	0
	0.3	0.31	3614	746	1549.4	23.42
	0.0	0.00	NA	746	1679.8	32.09
Skukuza	1.0	0.85	1402	553	3090	0
	0.3	0.29	2417	553	2632	23.05
	0.0	0.01	NA	553	2973	27.01
Satara	1.0	0.63	2146	547	2869	0
	0.3	0.25	2577	547	3766	23.41
	0.0	0.00	NA	547	2494.7	26.95
Mopane	1.0	0.55	1341	496	2909	0
	0.3	0.26	1686	496	2496	24.59
	0.0	0.01	NA	496	2829	31.24

The most northern plots are dominated by *Colophospermum mopane* and occur on clay basaltic soils (Mopane plots). Further south are the Satara-plots, also on clayey basaltic soils. The woody component of these Satara plots is dominated by *Sclerocarya birrea* and *Acacia nigrescens*. Further south again is the *Combretum spp.* landscape type (Skukuza-plots), on sandy granitic soils. The woody component in these plots is mainly dominated by *Combretum collinum* and *Combretum zeyheri*. The most southern plots occur on sandy granitic soils (Pretoriuskop-plots). The vegetation is dominated by dense, tall *Terminalia sericea* stands.

Sampling

We measured the clustering of trees in savanna areas using the T-squared sampling method (Hines & Hines 1979). This method measures 2 distances: the distance from a random sample point (+ in Figure 3.3A and 3.3B) to the closest tree ("distance A", Figure 3.3A), and the distance from that tree to its nearest neighbour ("distance B", Figure 3.3A), with the restriction that the angle between distances A and B is minimally 90°.To distinguish whether trees are "actively" or "passively" clustered, we created 2 datasets. For each dataset, "distance B" was measured differently.

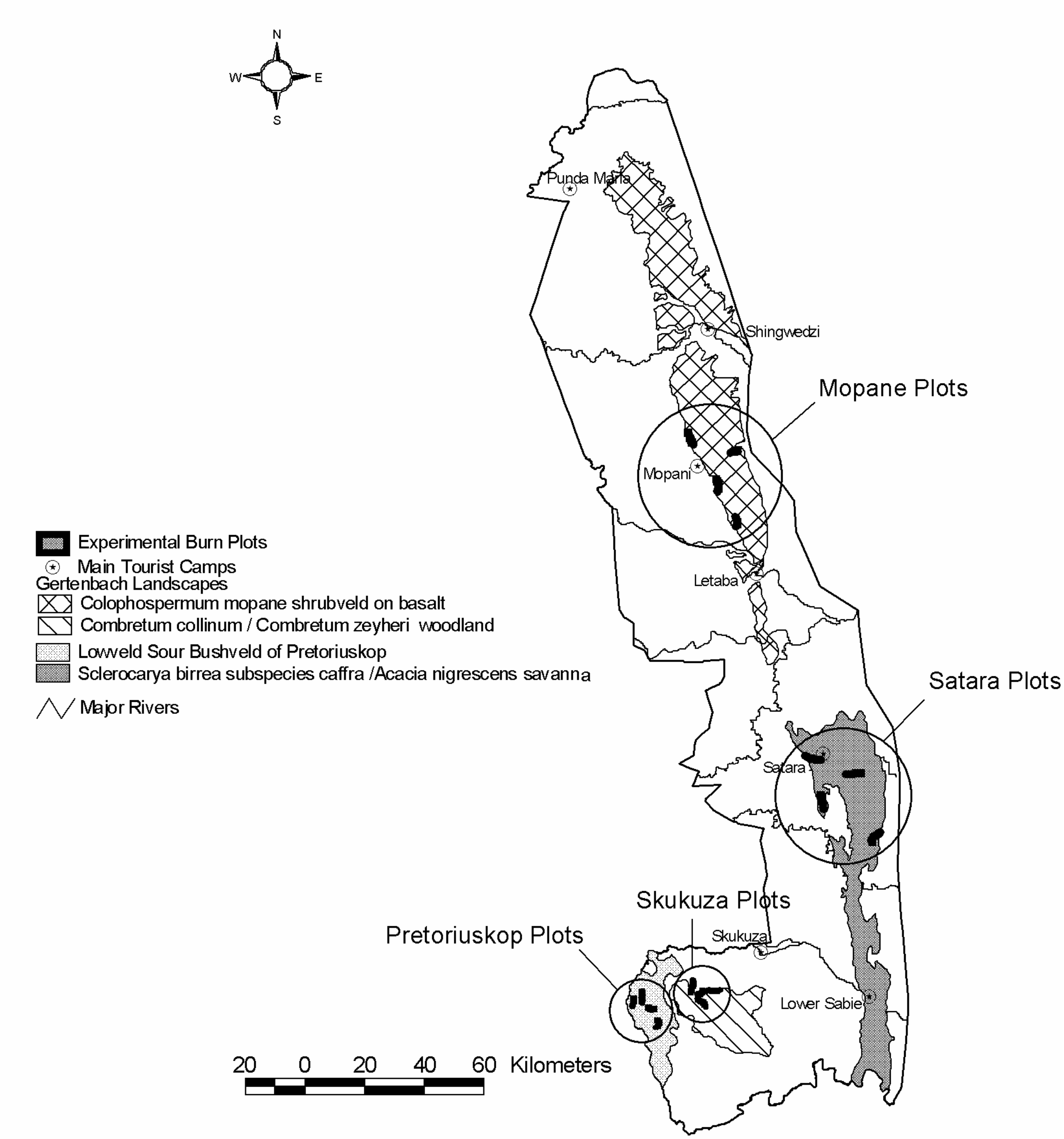


Figure 3.2 Map showing the locations of the experimental burning plots of the Kruger National Park in South Africa (after Biggs *et al.* 2003).

For “passive clustering”, an “any species” dataset was created where “distance B” was measured to the nearest neighbour of the tree without consideration of the species of this nearest neighbouring tree. For “active” clustering, a “same species” dataset was created where “distance B” was measured to the nearest neighbour of the tree of the same species. These distances can be the same when the nearest neighbouring tree is of the same species; otherwise, the distance for the “any species” dataset will always be shorter than the distance for the “same species” dataset.

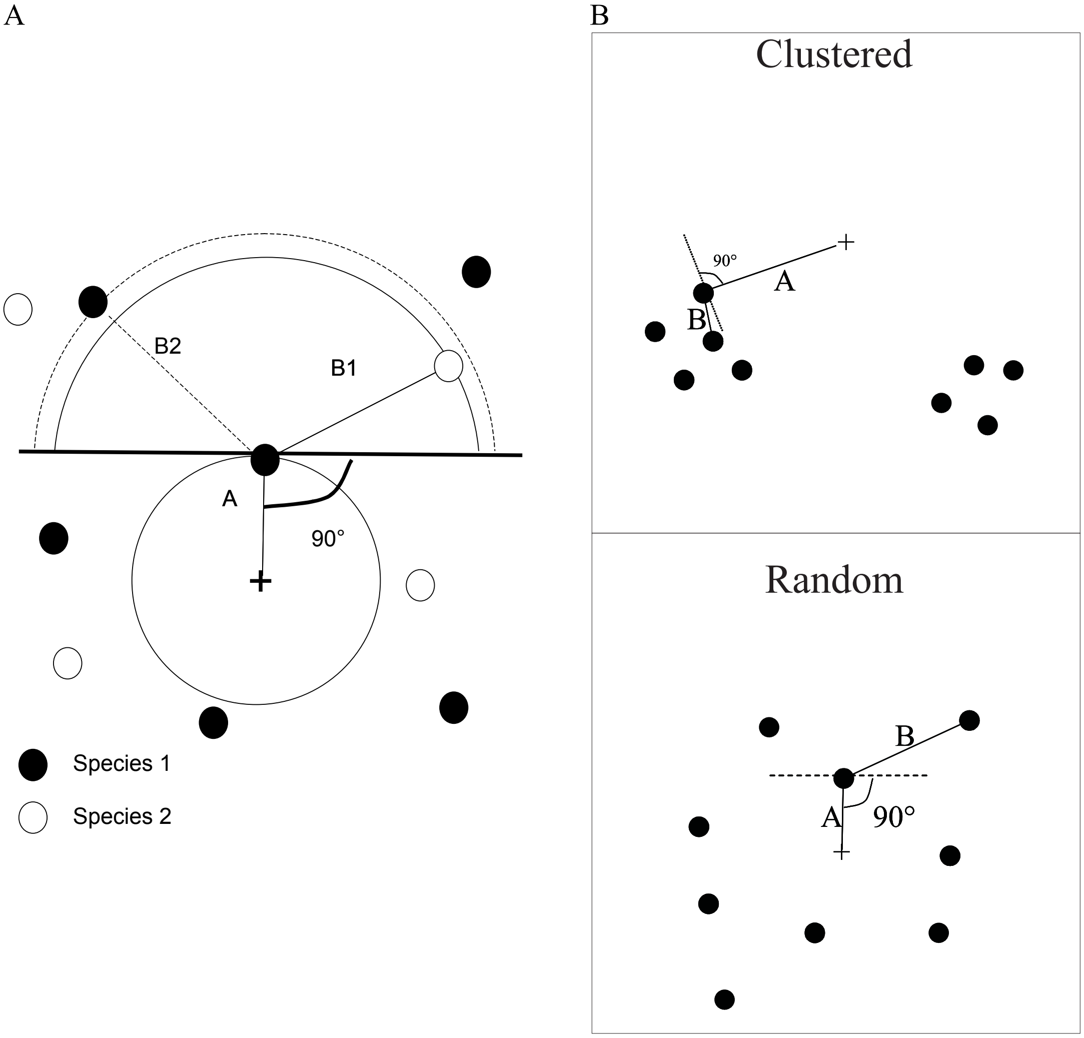


Figure 3.3 (A) Graphical representation of the T-square sampling method, (B) the distribution of trees (points) in a clustered and a random fashion.

Of all three trees that were included in the sample, tree species, height, canopy diameter, dominant grass species under the canopy and whether the tree was on a termite mount was recorded. Also, as an indicator of herbivore effects, the presence of damage from browsing (*e.g.*, minor bark damage) or elephants (*e.g.*, uprooting and breaking off of high branches) on the trees was recorded for each tree. Because we tested the effect of clustering of established trees, only trees of 1.5 metres in height or higher were incorporated in the sampling. In each plot 40 sample points were taken, resulting in 120 measured trees per plot. Furthermore, a soil sample was taken at each sample point and manually classified as sand, loam or clay (Euroconsult 1989). Distance between the sample points was 20 metres on average, but varied according to the density of trees in the plots. In total, 2350 points were sampled in 48 plots, distributed over three different fire regimes and four different landscape types.

Variables

If trees have a random distribution, then on average “distance A” should be similar to distance B, while in a clustered environment “distance A” should be larger than “distance B” (Figure 3.3A). Therefore, we used the ratio of “distance A” and “distance B” as a proxy for the clustering of trees. Larger values of this ratio indicate a more clustered distribution. This ratio was calculated for both the “any species” dataset and the “same species” dataset. To prevent a skewed distribution, the natural logarithm of the ratio was used and subsequently the average of this value for each plot was calculated, yielding 48 data points. This clustering index at the plot level will be further referred to as *C*.

How fire affects clustering of savanna trees is largely dependent on its intensity and flame height, determined by grass biomass as fuel load and local weather conditions. However, the grass composition can also play a role. A grass species that should be specifically mentioned for the Kruger National Park is guinea grass (*Panicum maximum*), which is considered to hamper fire intensity (Grice & Slatter 1996, Howard 2000, Wallmer 1994). It grows abundantly under tree canopies, while being relatively scarce outside tree canopies (Gibbs Russel *et al.* 1990, Tainton 1999). The frequency of times that *P. maximum* was the dominant grass species was calculated per plot.

Termite mounds were included in the analyses, because they are known to provide a different micro habitat, with for example a higher nitrogen content than the surrounding soil (Joquet *et al.* 2005), or with less grass biomass. We calculated the frequency of trees in a plot that were situated on a termite mound.

A tree species that is important to mention separately is the mopane tree (*Colophospermum mopane*), which is known to occur in dense monospecific stands as result of clonal growth and regeneration (Wessels 2001). Because of its dominance in some parts of the research area, it can obscure overall trends, and therefore it was included in the analyses. To do so, we calculated the frequency of the occurrence of *C. mopane* in each plot.

For the same species dataset the tree species diversity can potentially have an effect on the clustering index. When measuring nearest neighbour distances for same species in a tree community that is dominated with one species, nearest neighbour distances will be on average shorter then when measuring in more diverse tree communities. To control for this we determined the number of different tree species in each plot and the Shannon’s diversity index which is calculated as:

$$I = -\sum_{j=1}^{S} p_j \ln p_j$$

in which I is Shannon’s diversity index, p_j is the frequency of tree specie j in our sample and S is the total number of tree species in the plot. Higher values for I indicate a higher diversity of tree species.

For each burning treatment, long-term (±20 years) data are available on fire frequency, grass biomass (fuel load) and distance to waterholes (KNP Scientific Services 2005, Table 3.1). However, deviations from the intended fire frequencies have occurred. Sometimes plots were accidentally burnt by runaway fires or, contrastingly, burning could not take place because the vegetation was too wet or not abundant enough. For our analysis, we used the actual fire frequency, which is the total number of burns on a plot since 1954 divided by the number of years that the experimental burning program was running (*i.e.*, 52 years). Data on actual fire frequencies were retrieved from Biggs *et al.* (2003). Additionally, data on the moisture content of the biomass during burning events and the average intensity of fires—both averaged over all burning events—were included in the analyses as indicators of the severity of the fire history.

Data on distance to water points were used as a proxy for grazing pressure, complemented with the data on browsing and elephant damage. For the presence of browser damage and elephant damage the frequency of occurrence for each plot was calculated. For each plot, the average clay content and average tree height was calculated. Finally, the landscape types in which the plots were located were included as dummy variables in the analyses as well as the mean annual precipitation.

Analyses

To investigate what determines clustering of savanna trees, we performed a backward stepwise linear regression with *C* as dependent variable on both the same species dataset and the any species dataset. We included both the main effects of possible processes affecting clustering of trees as well as their interaction with fire.

The effect of distance between nearest neighbours on the impact of fire was tested by applying linear regression to the distance between nearest neighbours and canopy diameter (as in Smith & Goodman 1986). Regression was performed separately on data from control plots, plots with annual burning and plots with tri-annual burning. Regression coefficients (*i.e.*, slope and intercept) were tested for significant differences among burning regimes, using the Tukey test as described in Zar (1996).

Table 3.2 The selected models for both datasets. Both direction and significance levels are given for each variable, as well as the overall model performance in terms of significance and R^2_{adjusted}.

Any species dataset			Same species dataset		
Variable	*Sign*	*P*	*Variable*	*Sign*	*P*
Average clay content in the soil (%)	+	<0.001	Interaction between average clay content of the soil and fire frequency ($\% \text{ yr}^{-1}$)	+	<0.001
			Interaction between distance to the nearest water point and fire frequency (m yr^{-1})	-	0.018
			Shannon's index (-)	-	<0.001
			Average fuel load (kg ha^{-1})	+	0.082
			Distance to the nearest water point (m)	+	0.041
			Fire frequency (yr^{-1})	+	0.026
			Fuel moisture content ($\%_{\text{mass}}$)	-	0.010
			Fraction of trees on termite mounts (%)	+	0.034
$R^2_{\text{adjusted}} = 0.3184$ $P_{\text{full model}} < 0.001$			$R^2_{\text{adjusted}} = 0.7977$ $P_{\text{full model}} < 0.001$		

Results

The models selected by backward selection are displayed in Table 3.2. Both models were significant, and the R^2 adjusted was 0.32 for the any species dataset and 0.80 for the same species dataset. Two interaction terms with fire were included in the model. Because interactions are usually difficult to interpret, we show the trends of clustering for all the included interaction terms in Figure 3.4.

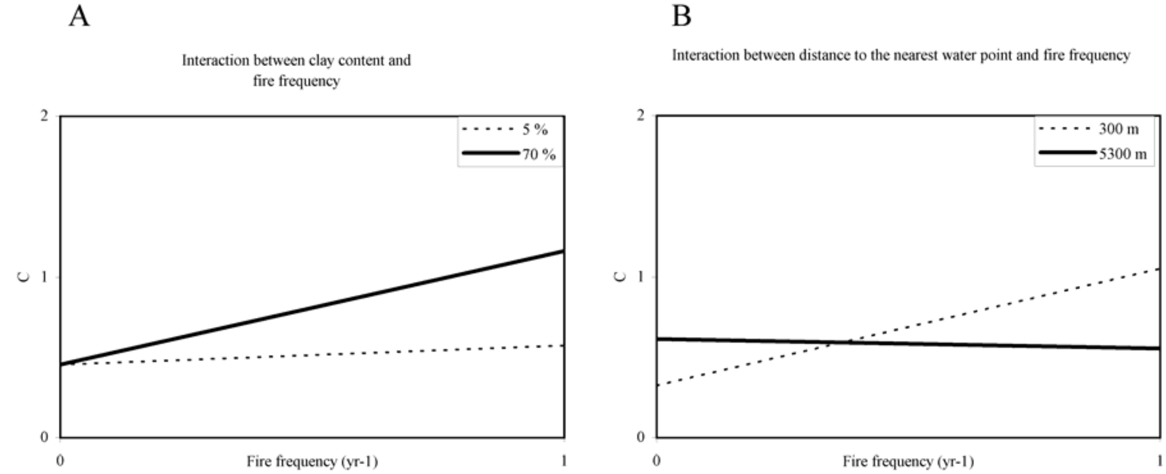


Figure 3.4 Interactions between fire frequency and other variables for the models selected with backward selection for the "same species" dataset. Interactions are shown for (A) fire frequency and average clay content in the soil and (B) fire frequency and the distance to the nearest water point. The model used included all significant explaining variables. Average values as measured in the field were used for the explaining variables that are not plotted in the graph, and the ranges for the shown variables are based on the minimum and maximum values for these variables as found in the field.

For the same species dataset much more variables were included compared to the any species dataset. For the any species dataset only clay content in the soil was included as variable, which is positively correlated with *C*. Fire had a significant positive effect on the clustering of the same species dataset. The first interaction term included is the interaction between fire frequency and clay content in the soil which is also positive, which indicates that the clustering effect of burning is enhanced at locations with high clay content values (Figure 3.4A). The second interaction term included is between distance to the nearest water point and fire frequency. Together with the main effect of distance to the nearest water point, this interaction diminishes the clustering effect of burning with increasing distance from water holes as shown in Figure 3.4B. Average fuel load has a positive effect on clustering and the fuel moisture content has a negative effect on the clustering of the same species dataset. Shannons' index correlated negatively on the clustering of the same species dataset. Finally the presence of termite mounds had a positive correlation with clustering in the same species dataset We found relationships for the distance between nearest neighbours and canopy diameters for three different fire management regimes (Figure 3.5). Estimated slopes were significantly different between the control plots and the plots with annual or tri-annual burning ($P<0.05$ and $P<0.001$, respectively), but not between the annual and tri-annual regimes ($0.2 < P < 0.5$).

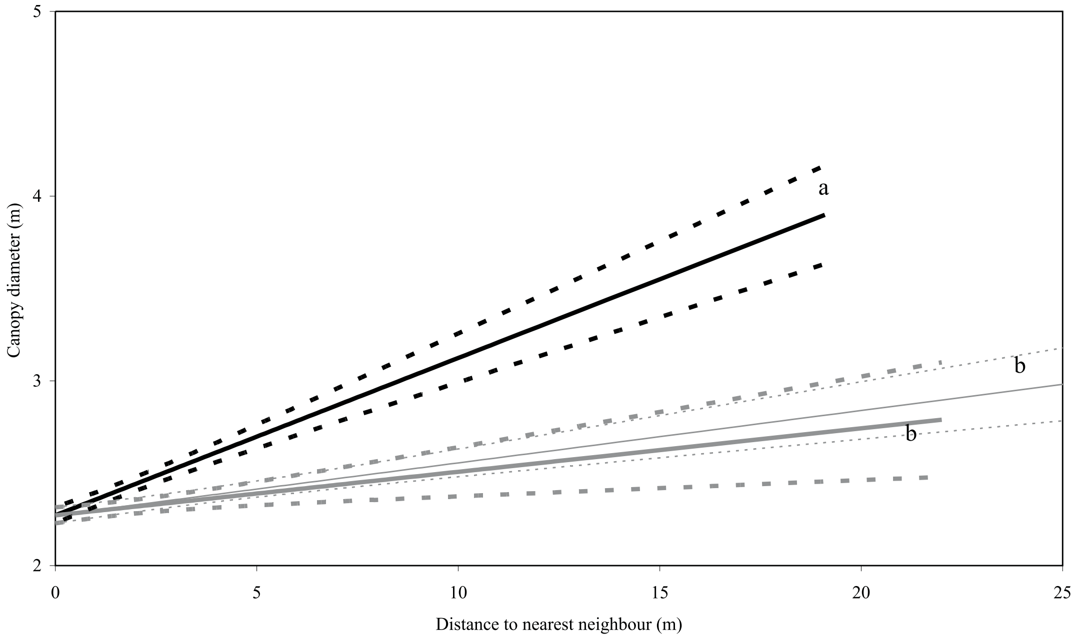


Figure 3.5 Fitted regression model (solid lines) and the 95% confidence limits (dashed lines) for the relationship between nearest neighbour distance and canopy diameter. The bold black line is fire frequency =0, the bold grey line fire frequency = 0.3yr^{-1} and the thin grey line fire frequency = 1yr^{-1}. Letters (a & b) indicate significantly ($P<0.05$) different slopes.

Discussion

Determinants of tree clustering

In this paper, we show that fire has a positive effect on tree clustering, in the case of clusters composed of a single species. Supplementary fire indices like the average fuel load and the fuel moisture content support this observation. An increasing fuel load implies higher fire intensities, and through that a more effective impact of burning on individual trees. We found a positive effect of fuel load on clustering in the same species dataset. Fuel moisture content on the other hand has a negative effect on the impact of burning as high moisture content values imply lower burning temperatures. We found a negative effect of fuel moisture content on clustering in the same species dataset.

The result that a significant effect of burning on clustering could be found for the "same species" dataset, but not for the "any species" dataset suggests that the effect of burning on clustering is much stronger for the "same species" than for the "any species". We can possibly explain this as follows. Suppose clustering is an "active" process due to limited dispersal for some but not all tree species (*i.e.*, there are "actively clustering" species and "non-clustering" species), and that no burning takes place. Then, one would expect a mix of clustering and non-clustering tree species to occur. However, when fires occur in this system and isolated trees have a higher probability of being killed by fire than do trees in a cluster, then trees that are not protected in a cluster are killed (the "non-clustering" tree species), while "actively clustering" tree species would survive. When measuring clustering in such a system, the clustering ratio without fire would yield an average value because trees both within and outside a cluster are encountered: trees inside clusters return relatively high ratio values, and trees outside clusters relatively low ratio values. This agrees with our findings for the "any species" data set. Measuring clustering for trees for the "same species" dataset will result in a very low clustering ratio because for "non-clustering" species their nearest same species neighbour would then be much further away than the nearest neighbour of “any species”. When measuring these same values but now in a system where burning takes place frequently, the “non-clustering” species would not be present and only the “actively clustering” species are present, yielding similar values for both the “any species” and “same species” datasets. This results in a very strong effect of fire on clustering in the “same species” dataset and a weaker effect in the “any species” data set.

However the effect of burning is not only related to fire occurrence, but also influenced by environmental variables. In our analysis clay content of the soil, and distance to the nearest water point are included as determining factors. In fact, average clay content in the soil was the only explaining factor for the “any species” dataset, while it contributes to the interaction with fire occurrence for the “same species” dataset. This could be due to the higher water retention capacity of clayey soils. With sufficient rainfall, higher clay content results in higher water availability in the top layer of the soil. With high water availability at the surface, tree seedlings will establish more easily near mother trees that are at the same time competing for water. This suggests that clustering occurs through the “active” dispersion effect of plants (Pacala & Levin 1997).

The distance to the nearest water point has a negative effect on the clustering of trees in the “same species” dataset. We assume that with increasing distance to water the impact of herbivores on the vegetation diminishes. It is well possible that through disturbance of herbivores, for example uprooting of trees by elephants, the impact of burning becomes more effective because the area is kept open and fires are less hampered by shrubs. The impact of herbivores has been investigated in other studies (Prins & Van der Jeugd 1993, Van de Vijver *et al.* 1999, Goheen *et al.* 2007), showing strong significant effects on the structure of woody plant communities. Also the interaction between herbivory and fire has been shown in previous studies (Van Langevelde *et al.* 2003, Archibald *et al.* 2004). This study shows that the interaction between fire and herbivory does not only determine the tree grass balance, but also the spatial configuration of the trees.

Because the assembling of the “same species” dataset could potentially be influenced by the tree species diversity we used the Shannon’s index as a measure of species diversity. This variable was retained in the backward regression. Shannon’s index can be interpreted as the effective number of tree species in the area, given the distribution of different tree species, and is negatively correlated with clustering. This would make sense, as with higher species diversity, the chances to find a same species nearby will become less. However, when controlling for this variable (by including it), the other variables still have an important effect on the clustering of the “same species” dataset.

The last variable that was retained in the model is the occurrence of termite mounts in the plots. This was positively correlated with clustering. Termite mounts are known to have higher nutrient content, which might facilitate the settlement of saplings. Also, when termites are of a grass harvesting species, the occurrence of fires and the competition with grasses is reduced, improving settling success of saplings. This could facilitate the “active” clustering of tree species.

Because tree density affects distances between trees, increased clustering could be expected at higher tree density. When correlating tree density and the clustering of trees, we found, however, that our measure for the clustering of trees is not correlated with tree density (data not shown, P>0.05).

Effects of nearest neighbour distances on impact of fire

As clearly shown in Figure 3.5, fire has a pronounced effect on the relationship between distance to the nearest trees and their canopy diameter. The relationship agrees with the hypothesis as formulated in Figure 3.1B. Fire reduces the size of individual tree canopies more

when they are further apart than when they are close together. This suggests that trees might protect each other from the effects of fire, and that as distance increases, the protective effect of surrounding trees diminishes.

These findings complement the findings of Smith and Goodman (1986), who found that an increase in either soil nutrients or water resulted in an increase in the slope of the relationship between the nearest neighbour distances and canopy diameter. In our study, an increase in fire resulted in a decrease of this slope.

Conclusion

This study has shown that clustering of savanna trees can be attributed to several factors including fire frequency, soil clay content, species composition. The availability of water and effects of competition on seedling establishment seem to be important factors determining whether trees occur in clustered patterns. Also, our results suggest that clustering is most likely an “active process” that occurs through the recruitment of seedlings close to the mother plant. Finally, the results have shown that trees can protect each other from the negative effects of fire. These results contribute to our understanding of savanna functioning in that they show which processes are relevant in the distribution of trees in savannas. This distribution, in turn, can influence the impact of spatial processes such as fire, as suggested by our results which showed that shorter distances to nearest neighbour trees indeed lowered the damaging effect of fire.

Acknowledgements

This study was partially financed by donations from a WOTRO travel fund and the Schure Beijerinck Popping Fund to T.A. Groen. We would like to express our gratitude to KNP Scientific Services for logistic support, J. Baloy, T. Mabasa and T. Keswick for field assistance, and R. Grant and H. Biggs for useful input on the set-up of the research. Comments from three anonymous reviewers greatly improved the statistical analysis as well as the overall manuscript, for which we are grateful. Finally we would like to thank E. Tynan for reviewing the manuscript on English.

BOX 3.1

The interaction between the diameter of clusters of woody species and fire intensity

THOMAS A. GROEN, LAURA A. VONK, WINSTON, S.W. TROLLOPE, CLAUDIUS A.D.M. VAN DE VIJVER & FRANK VAN LANGEVELDE

Introduction

Fire plays a major determining role in the dynamics of the savanna ecosystem (Bond & Van Wilgen 1996, Van de Vijver 1999, Van Langevelde *et al.* 2003). The major fuel for fires in savannas is grass biomass, which carries the fire through the landscape (Shea *et al.* 1996). Woody species, however, are also affected by these fires, as fires remove plant biomass indiscriminate to their palatability, unlike herbivory (Bond & Keeley 2005). The amount of biomass removed by fires is influenced by other factors. An important factor is the intensity of the fire, which is the amount of energy released by the fire per unit time. The intensity is mainly determined by the (micro-) climatic conditions during the fire and the amount of fuel present in the system. But the effect of burning also depends on individual plant traits of woody species like the water content of the plant tissue, bark thickness (Hoffman *et al.* 2003) and the size of the plant. In previous research it has been shown that damage to woody species reduces when plants grow taller (De Ronde *et al.* 2004). For woody plants however, height is not their only size characteristic, and their canopy diameter can potentially affect fire impact as well, because the width of a canopy might determine whether there is a significant difference in micro-climatic conditions between the leeward and windward side of the tree. Also, some woody species form dense clusters, excluding fire in their interior, which might have the same effect on micro-climatic conditions as a single isolated tree.

The mechanism that is expected to cause variation in the impact of fire on woody species as a result of their diameter is the effect these clusters can have on micro climatic conditions. These micro climatic conditions, in turn, determine the fire intensity, which is an important factor regulating the damage of fires to woody species. The major climatic variables that determine fire intensity are relative humidity, ambient temperature and wind speed (Govender *et al.* 2006, Trollope *et al.* 2004). Especially wind speed is expected to be influenced by cluster sizes. Clusters of woody species can form barriers that provide on the leeward side different climatic conditions than on the windward side. As clusters grow larger, their wind blocking capacity is expected to increase and with that their effect on micro climatic conditions on the leeward side. However, what the exact effect of cluster diameter is on the intensity of fire is so far unknown. We performed an experimental study to investigate the effects of cluster size on fire intensity. Our hypothesis is that with increasing cluster size, fire intensity at the leeward side is reduced.

Methods

To measure the effect of cluster diameter on fire intensity we performed a burning experiment at the experimental farm of the University of Fort Hare in the Eastern Cape, South Africa. We measured fire intensity at the lee- and windward side of artificial clusters with varying diameter sizes. These artificial clusters were placed in homogeneous grass swards, and fires were ignited from a fixed distance (10m) from the artificial clusters at the windward side.

We constructed artificial clusters out of sheet metal. The sheets were 1.2 meters in height, and were placed in a circle with diameters of 1m, 3 m, 7m and 10m as shown in Figure 3.1.1. We chose for artificial clusters rather than natural woody clusters, because this allowed us to control for the exact position of the clusters in the field in relation to the wind direction, and to control the range of different sizes. In total nine experimental fires were successful and in each fire, all four artificial cluster sizes were included (as shown in Figure 3.1.1).

Figure 3.1.1 Realisation and lay out of the artificial bush clumps in the field.

At the lee- and windward side of the artificial clusters we measured fire intensity in a different way than is custom in fire ecological studies. We measured fire intensity at point locations, making use of thermocouples that were connected to data loggers that can record temperatures every second. We placed three thermocouples in a triangle pointing away from the artificial cluster at each side of an artificial cluster, so that two thermocouples would be near the artificial cluster and one would be further away from the artificial cluster. The thermocouples yielded time series on the air temperature at the lee- and windward sides of the artificial clusters.

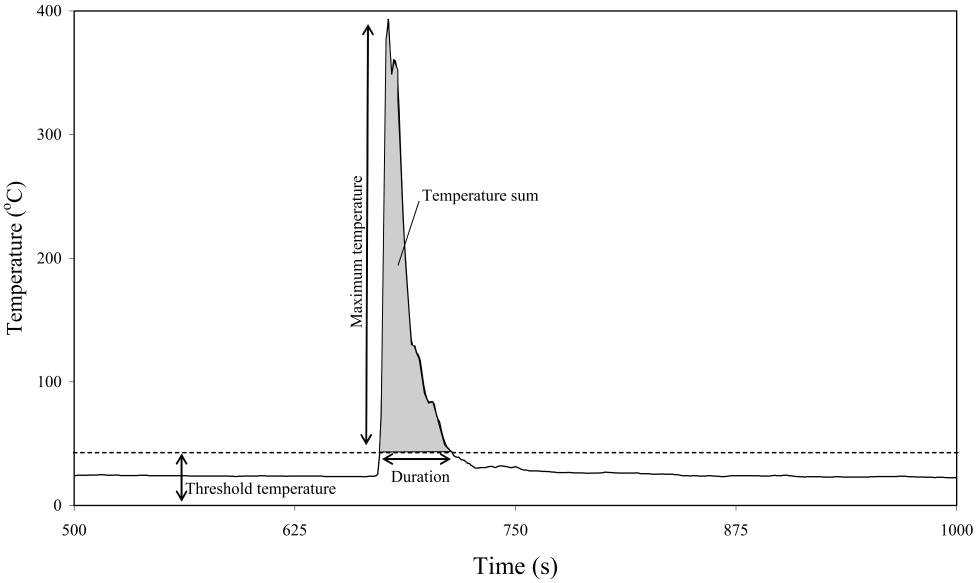


Figure 3.1.2 An example of a temperature time series as measured in the field. Three fire intensity estimators are extracted from this figure, maximum temperature, the duration of the fire, and the temperature sum (see text).

From the time series measured during the burning treatments, three fire intensity estimators were extracted, maximum temperature of each measurement series (˚C), duration of the fire (s) and the temperature sum (s ˚C), as depicted in Figure 3.1.2. For both the duration of the fire and the temperature sum we made use of a threshold temperature. This threshold temperature was used to determine when the fire started and ended, as well as to see what the added effect of the fire was on the ambient temperature. However, because temperatures were not equal every day that an experimental burn was carried out, we fixed the threshold temperature at 40˚C for each measurement.

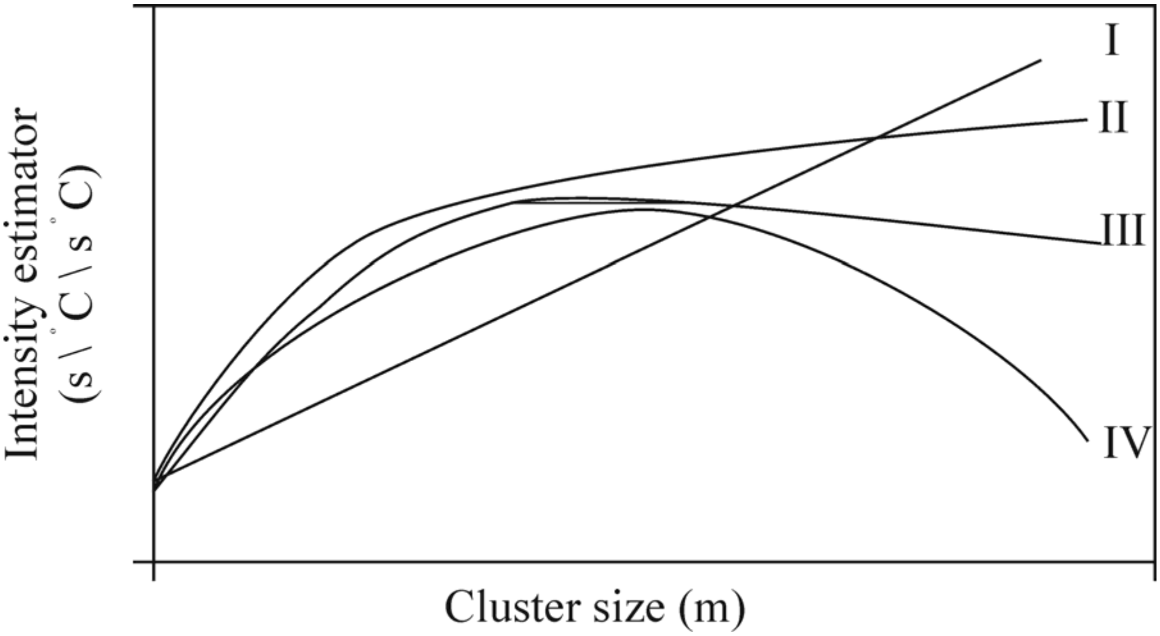


Figure 3.1.3 The four different types of models fitted through the data; linear (I), saturating (II), hump shaped that decreases to an asymptote (III) and parabolic (IV).

Possible explaining variables for the intensity estimators that were measured in the field were: grass biomass near the thermocouple, average grass cover in the plot, average moisture content of the grass in the plot, ambient temperature during the fire, wind speed during the fire and relative humidity during the fire. As control factor we included the distance of the thermocouples to the artificial clusters. Finally we included the size of the artificial clusters, the squared size of the clusters and the interactions between cluster sizes and the other explaining variables in the analysis.

Table 3.1.1 The “minimal” models fitted through the diameter size-fire intensity estimator data.

Description	Equation
Linear	$Y = aX + b$
Saturating	$Y = \frac{aX}{b + X}$
Hump shaped	$Y = \frac{aX}{b + X + cX^2}$
Parabolic	$Y = aX + bX^2$

We used both forward and backward multiple stepwise regressions to analyse the relations between the different explaining variables for the three depending variables. Both temperature sum and duration of the fire were logarithmically transformed before the analysis, to obtain normally distributed residuals. Besides multiple stepwise regressions we also fitted four different curves through the data with only cluster size as explaining variable, which we will call the minimal models. The types of models that were compared were a linear model, a saturating model, a hump shaped model that decreased to an asymptote and a parabolic model (Figure 3.1.3,Table 3.1.1). We compared the Akaikes information criteria (AIC) of these models to decide which of the four models fitted the data best.

Results

The results of the analysis are shown in Table 3.1.2. Forward and backward stepwise regression procedures yielded the same models for each of the three depending variables. All models found were significant, and explained between 47% and 75% of the variation in the dataset. For all three analyses, the size of the clusters, and the squared size of the clusters were included. The positive effect of the cluster size and the negative effect of the squared cluster size for each of the tested depending variables suggest a parabolic response for each of these variables to cluster size (model IV, Figure 3.1.3).

Table 3.1.2 The results of the forward and backward regressions and the minimal model fitting (see text).

	Depending variables					
	Log temperature sum (s ^oC)		Maximum temperature (^oC)		Log duration of the fire (s)	
	Stepwise regression models					
Explaining variables	sign	P	sign	P	sign	P
Intercept		<0.001		<0.001		<0.001
Cluster size	+	<0.001	+	<0.001	+	<0.001
(Cluster size)^2	-	<0.001	-	<0.001	-	0.001
Cluster size * Moisture content			-	0.028		
Moisture content	-	<0.001	-	0.029	-	<0.001
Cluster size * Relative humidity	-	0.035			+	0.030
Relative humidity	-	<0.001	+	0.007	+	<0.001
Cluster size * Ambient temperature					+	<0.001
Ambient temperature	-	<0.001			+	<0.001
Wind speed	-	<0.001	+	0.003	-	<0.001
(Wind speed)^2	+	<0.001				
R^2 adjusted	0.75		0.47		0.74	
P model	<0.001		<0.001		<0.001	

Minimal models

	AIC	AIC	AIC
Linear model	$7.40\ 10^0$	$1.94\ 10^3$	$-1.31\ 10^2$
Saturating model	$7.73\ 10^2$	$2.16\ 10^3$	$4.88\ 10^2$
Hump shaped model	$7.39\ 10^2$	$2.16\ 10^3$	$4.90\ 10^2$
Parabolic model	$-1.76\ 10^0$	$1.92\ 10^3$	$-1.31\ 10^2$

The comparison of the four minimal models is also presented in Table 3.1.2. Lower values for AIC indicate better fits. For all three depending variables tested, the parabolic model and the linear models performed better than the hump shaped and saturating model. Both linear and parabolic models are displayed in Figure 3.1.4.

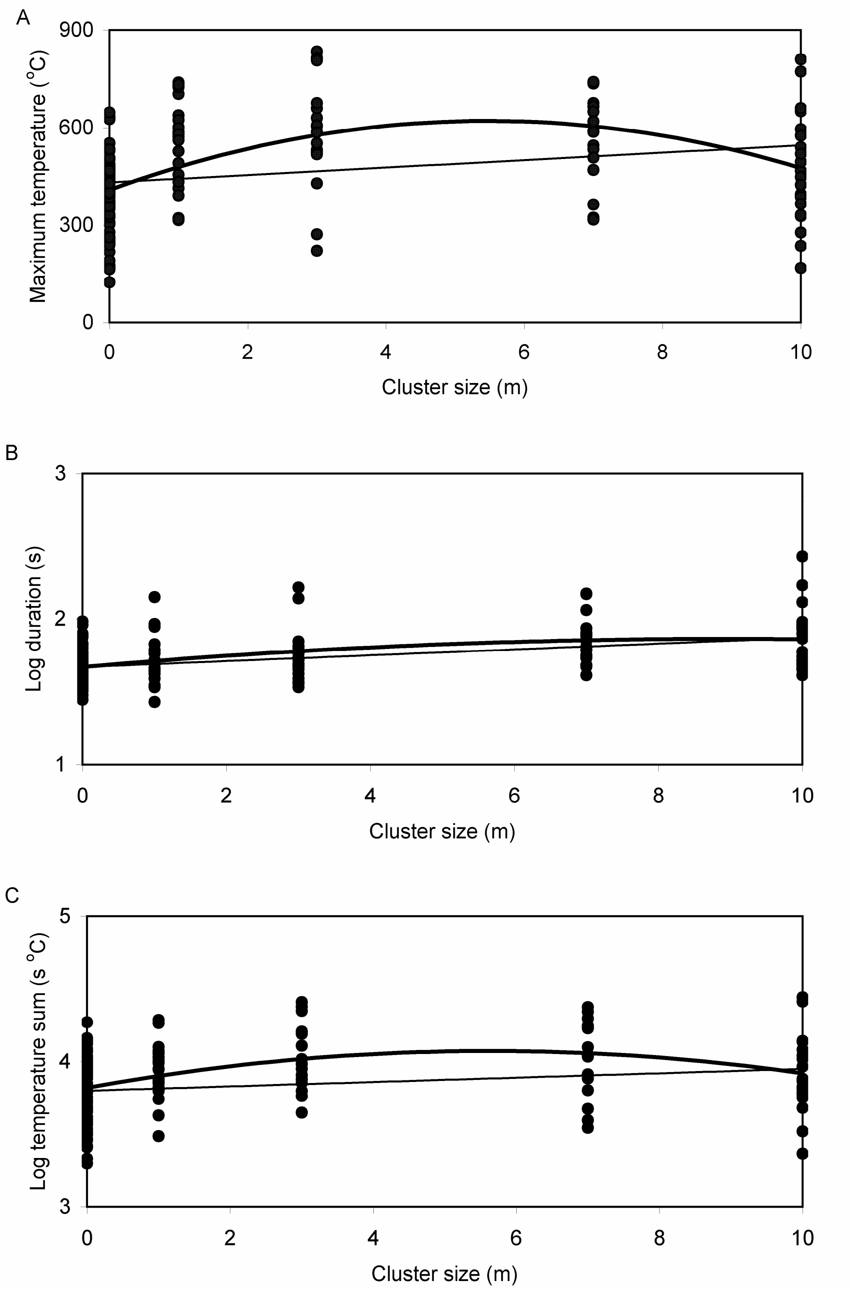


Figure 3.1.4 Maximum temperature (A), the log of the duration of the fire (B) and the log temperature sum (C) as fire intensity proxies and their response to increasing cluster diameter. Bold lines show the parabolic models and thin lines the linear models.

Conclusion & discussion

The found trends between cluster size and the intensity estimators had an opposite direction than expected. We expected a single linear negative trend, *i.e.*, that with increasing diameter sizes of the clusters, the intensity of fires at the lee side would decrease. In stead we found that a linearly increasing or parabolic function fitted the data best. This suggests that clusters actually have a positive effect on fire intensity on the leeward size. Possibly this can be due to different moderation of the micro-climatic conditions on the leeward side, than expected. We expected that wind speed would be lower at the leeward side of the clusters, but maybe due to aerodynamic properties of the clusters, wind speed is actually higher at the leeward side. Maybe, clusters can only effectively block the wind at a minimum size, which is larger than the range that we covered with our artificial clysters. In that case, it would be expected that at very large cluster sizes the positive effect of clusters on fire intensity would diminish, which is also suggested by the parabolic model, that fits equally well through the data.

Although the artificial clusters were a convenient approach to control for variability in cluster size and the position of clusters in the landscape, one can wonder whether the artificial clusters capture the essence of real clusters of woody species with respect to their fire suppressing capacities, as well as their moderating effect on the micro climatic conditions at the leeside of the woody clusters. A first step would be to measure the different micro climatic differences between leeward side and windward side of woody clusters, and compare them with the differences for our artificial clusters. Therefore the results presented in this study must be interpreted as an initial step in unravelling the dynamics of clusters in savannas and their interaction with fire. Finding the same relation with real clusters of woody species would be needed however to increase the confidence in the results presented in this study.

CHAPTER 4
Herbivores as architects of savannas: inducing and modifying spatial patterning

HENRIK J. DE KNEGT, THOMAS A. GROEN, CLAUDIUS A.D.M. VAN DE VIJVER,
HERBERT H.T. PRINS & FRANK VAN LANGEVELDE

Abstract

In this paper, we address the question through which mechanisms herbivores can induce vegetation patterning in savannas, and how the role of herbivory as a determinant of vegetation patterning changes with different pre-existing vegetation patterns. We developed a spatially explicit simulation model, including growth of grasses and trees, vertical zonation of browseable biomass, and spatially explicit foraging by grazers and browsers. Herbivore densities were kept constant. We show that herbivores can induce vegetation patterning when two conditions are satisfied. First, they have to increase the attractiveness of a site while foraging so that they revisit this site, *e.g.,* through an increased availability or quality of forage. Second, foraging at a site should influence vegetation at larger spatial scales. These two conditions operating simultaneously proved to be crucial for herbivores to produce spatial vegetation patterns, but then only at intermediate herbivore densities. High herbivore densities result in homogenous vegetation. Furthermore, our model shows that the influence of the pre-existing vegetation pattern on the role of herbivores decreases when the heterogeneity and scale of patchiness of the initial vegetation decreases, caused by an increasing level of adherence of the herbivores to forage in larger pre-existing patches. The findings presented in this paper, and critical experimentation of their ecological validity, increases our understanding of heterogeneity and vegetation patterning, and the role of plant-herbivore interactions therein.

Keywords: *vegetation patterns, herbivory, self-facilitation, spatial foraging, foraging distribution, tree-grass patterns.*

Introduction

Savanna ecosystems, characterised by a continuous layer of grass intermixed with a discontinuous layer of trees and shrubs, are among the most striking vegetation types where contrasting plant life forms co-dominate (Scholes & Archer 1997). Factors regulating the balance between these life forms include rainfall, soil types, disturbances (*e.g.,* herbivory and fire) and their interactions (Greig-Smith 1979, Huntley & Walker 1982, Archer 1990, Scholes & Walker 1993). Savanna vegetation is spatially heterogeneous and often shows patterning, frequently a two-phase pattern of discrete shrub or tree clusters scattered throughout grassland (Archer *et al*. 1988, Archer 1990, Couteron & Kokou 1997, Breshears 2006). Understanding the origin of such vegetation patterns is a central issue in ecology (Greig-Smith 1979, Archer 1990, Scholes & Walker 1993, Jeltsch *et al*. 1996, Couteron & Kokou 1997, Adler *et al.* 2001, Sankaran *et al*. 2004, 2005), as vegetation patterning can have important consequences for ecosystem functioning (Adler *et al*. 2001, Rietkerk *et al*. 2004). At large spatial scales, the key determinants of vegetation patterning in savannas include spatial differences in abiotic characteristics such as rainfall and nutrient availability (Greig-Smith 1979, Huntley & Walker 1982, Scholes & Walker 1993). On the other hand, herbivory, fire, water run-on and run-off processes and soil nutrient-organic matter dynamics are considered as important determinants of vegetation patterning at smaller scales (Greig-Smith 1979, Huntley & Walker 1982, Scholes & Walker 1993, Jeltsch *et al*. 1996, 1998, Van de Koppel & Prins 1998, Klausmeier 1999, Lejeune *et al*. 2002, Sankaran *et al*. 2004, 2005). However, the mechanisms behind vegetation patterning in savannas are still poorly understood (Jeltsch *et al*. 2000, Weber & Jeltsch 2000, Sankaran *et al*. 2004, 2005).

This particularly applies to the mechanisms through which herbivores are able to induce or modify spatial vegetation patterning in savannas. Although various studies have demonstrated that foraging by herbivores affects the tree-grass balance (*e.g.,* Scholes & Walker 1993, Jeltsch *et al*. 1996, 1998, Roques *et al*. 2001, Briggs *et al*. 2002, Van Langevelde *et al*. 2003), actual consequences of herbivory on savanna vegetation patterning have hardly been investigated (Adler *et al.* 2001). Since savannas support a large proportion of the world's human population and a majority of its rangeland and livestock (Scholes & Archer 1997) understanding the role of herbivores in vegetation patterning in these ecosystems is urgently required (Sankaran *et al*. 2005), moreover because savannas are among the ecosystems that are most sensitive to future changes in land use and climate (Sala 2000, Bond *et al*. 2003, House *et al*. 2003).

In this paper, we focus on the mechanisms through which herbivores induce or modify vegetation patterning in savannas. We distinguish the interactions of grazers and browsers with herbaceous and woody vegetation, respectively. We investigate two basic mechanisms that will be tested for their effect on patterning by herbivores: *self facilitation* and *spatially explicit foraging* (Adler *et al.* 2001, Cid & Brizuela 1998, Woolnough & Du Toit 2001, Prins & Van der Jeugd 1998). Self facilitation is the process where herbivores increase the attractiveness of patches by foraging. Self facilitation is a process that can be found in ecosystems when regrowth of forage is of better quality than older forage. For example, grass regrowth is often of better quality than standing grass biomass (Crampton & Harris 1969, Prins & Olff 1998). For leaves of woody species the quality of browseable material remains mostly constant (Woolnough & Du Toit 2001), although secondary compounds such as tannins increase with leaf age (Du Toit *et al.* 1990). Browsers however, can keep foliage in reach by keeping trees short, avoiding trees to grow out of reach and at the same time stimulating regrowth (Fornara & Du Toit 2007), and in that way facilitate the availability of forage (Prins & Van der Jeugd 1998). Spatially explicit foraging is the process where animals do not "just take the best bites" in an area, but select foraging patches based on the average quality of that patch and its surrounding patches, and not only forage strictly in those selected patches, but also in the surroundings of that patch (Cid & Brizuela 1998, Adler *et al.* 2001, Baraza *et al.* 2006). So far, the role of these two mechanisms on vegetation patterning has not been systematically investigated

Since the role of herbivory in vegetation patterning depends on the interaction between the spatial pattern of herbivory and the pre-existing spatial pattern of vegetation (Adler *et al.* 2001), we subsequently analyse the effects of the scale and heterogeneity of the initial vegetation pattern on the role of herbivores in vegetation patterning. Focussing only at the influence of herbivory while leaving out other determinants like fire, nutrient cycling or water redistribution and their possible interactions allows us to isolate the role herbivores can have in vegetation patterning. Hence, we aim at contributing to a better understanding of the role of herbivory as a determinant of spatial vegetation patterning in savannas.

The model

General structure of the model

We developed a spatially explicit, cell-based model that simulates vegetation dynamics in each cell, based on availability of and competition for resources between grasses and trees. We then introduced herbivores into the simulated landscape, both grazers, foraging only on grass, and browsers, foraging exclusively on trees. Our simulations were run in a landscape covering a lattice with 200 x 200 cells of 5 x 5 m. To avoid edge effects, the simulated landscape was torus-shaped. The maximum time span of each simulation run was 1000 annual time steps, but the simulation was finished when the state variables remained constant for 50 years. The dynamics, variables (Table 4.1) and analyses involved are discussed below.

Table 4.1 Parameters used in the model and their interpretation.

Name	Interpretation	Units	Values	Sources
w_t	Rate of moisture recharge in the grass root zone	mm m^{-2} yr^{-1}	See Eq. 1	Van Langevelde *et al.* (2003)
w_{in}	Annual amount of infiltrated water	mm m^{-2} yr^{-1}	560	
w_s	Rate of moisture recharge in the tree root zone	mm m^{-2} yr^{-1}	See Eq. 2	Van Langevelde *et al.* (2003)
α	Proportion of excess water that percolates	-	0.4	De Ridder & Van Keulen (1995)
β	Soil moisture content in the grass root zone above which water starts to percolate to the tree root zone	mm m^{-2} yr^{-1}	350	De Ridder & Van Keulen (1995)
H	Grass biomass	g m^{-2}	See Eq. 3	
r_H	Water use efficiency of grass biomass	g mm^{-1}	1	Gambiza *et al.* (2000)
θ_H	Rate of water uptake per unit grass biomass	mm yr^{-1} g^{-1}	0.9	Walker *et al.* (1981)
θ_W	Rate of water uptake per unit woody biomass	mm yr^{-1} g^{-1}	0.5	Walker *et al.* (1981)
W	Total aboveground woody biomass	g m^{-2}	See Eq. 4	Walker *et al.* (1981)
d_H	Specific loss of grass biomass due to mortality	yr^{-1}	0.9	Gambiza *et al.* (2000)
r_W	Water use efficiency of woody biomass	g mm^{-1}	0.5	Lamprey *et al.* (1980)

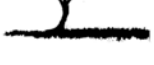


Table 4.1 continued (1)

Name	Interpretation	Units	Values	Sources
d_W	Specific loss of woody biomass due to mortality	yr^{-1}	0.4	Le Houérou (1980) and references within
L_{HH}	Loss of herbaceous biomass due to grazing	$g\ m^{-2}\ yr^{-1}$		
L_{WH}	Loss of woody biomass due to browsing	$g\ m^{-2}\ yr^{-1}$		
h_t	Total height	m	½ c_{nr}	-
h_b	Canopy bottom height	m	1/3 h_t	Caylor & Shugart (2004)
h_m	Canopy midpoint height	m	2/3 h_t	Caylor & Shugart (2004)
$c_{w,d}$	Canopy width at height *d* in the canopy	m	See Eq. 5	Caylor & Shugart (2004)
c_w	Canopy width	m	¾ h_t	Caylor & Shugart (2004)
d	Height in the canopy	m	0-10	
I_d	Light intensity at each layer *d* in the canopy	-	See Eq. 6	Huisman *et al.* (1997)
I_{in}	Index value for the incident light intensity above the canopy	-	1	
k	Light extinction coefficient of browseable biomass	-	0.2	
$W_{b,d}^{+}$	Total amount of browseable biomass above layer *d*	g		
Int_c	Amount of intercepted light of cohort *c*	-	See Eq. 7	
$W_{b,c,d}$	Amount of browseable biomass of cohort *c* at layer *d*	g		
req_p	Population requirements	$g\ yr^{-1}$	See Eq. 8	
f_d	Yearly food intake as proportion of body mass	-	9.125	Owen-Smith (2002)
P_{size}	Total population size measured by means of biomass	g		
I	Instantaneous food intake rate	$g\ min^{-1}$	See Eq. 9	
λ	Amount of grass removed by each bite	g		
i_{max}	Maximum food intake rate at high food abundance	$g\ min^{-1}$	20	
F	Food availability	$g\ m^{-2}$		
$g_{½}$	Food availability at which *I* reaches half of its maximum	$g\ m^{-2}$	100	
E	Instantaneous rate of energy intake	-	See Eq. 10	
q	Coefficient of the decrease in grass quality with increasing food availability	-	0.0019	Prins & Olff (1998)
w	Weighting factor of cells in the vicinity of cell *x*	-	See Eq. 11	
$dist$	Distance of the cell to cell *x*	nr cells		

Table 4.1 continued (2)

Name	Interpretation	Units	Values	Sources
wf	Exponent for the weighting of a cell	-	-3	
Γ(h)	Semi-variance at lag *h*	-	See Eq. 12	Treitz & Howarth (2000)
h	Distance on the ground between sample locations	m		Treitz & Howarth (2000)
N(h)	Number of pairs of observed data points separated by a lag of *h*	-		Treitz & Howarth (2000)
z	Value of the regionalised variable	*H, W*		

Resource availability

Following the majority of models that study savanna tree-grass balance and co-existence (*e.g.,* Walter 1971, Walker *et al.* 1981, Walker & Noy-Meir 1982, Eagleson & Segara 1985, Eagleson 1989, Higgins *et al.* 2000, Van Wijk & Rodriguez-Iturbe 2002, Fernandez-Illescas & Rodriguez-Iturbe 2003, Van Langevelde *et al*. 2003), we consider available moisture as the main resource limiting plant growth and neglect competition for nutrients. We used the two-layer hypothesis (Walter 1971) as the basis for water distribution in the soil and availability for tree and grass growth. This hypothesis assumes niche separation in the rooting zone of grasses and trees. Grasses are the superior competitors for moisture in the topsoil layer (*i.e.,* grass root zone), where both grasses and trees have roots. In the subsoil layer (*i.e.,* tree root zone), the competitive ability of trees is dominant, since only a negligible proportion of the grass roots penetrate to this depth (Weltzin & McPherson 1997, Schenk & Jackson 2002). Following Van Langevelde *et al*. (2003), we assume that all water that infiltrates in the soil on a yearly basis is available for the growth of grasses and trees. This infiltrated water first increases the soil moisture content in the grass root zone. Above a certain threshold, water starts to percolate from the grass root zone into the tree root zone. We assume that both rooting zones are not water saturated in savannas. The recharge rate of moisture in the grass root zone (w_t) can then be given by:

$$w_t = w_{in} - w_s \tag{1}$$

where w_{in} is the amount of infiltrated water per year and w_s is the rate of moisture recharge in the tree root zone (Van Langevelde *et al*. 2003, Table 4.1). The parameter w_s is proportional to the amount of infiltrated water:

$$w_s = \alpha(w_{in} - \beta) \qquad \text{if } w_{in} > \beta \qquad \text{else } w_s = 0 \tag{2}$$

where β is the soil moisture content in the grass root zone above which water starts to percolate to the tree root zone, and α is the proportion of excess water above β that percolates to the tree root zone.

Vegetation dynamics

The model features the vegetation components grass biomass (consisting of grasses and herbs) and woody biomass (consisting of wood, twigs and leafs of trees and shrubs). The rate of change of aboveground grass biomass *H* over one year can be calculated as follows (Walker *et al*. 1981, Walker & Noy-Meir 1982, Van Langevelde *et al*. 2003):

$$\frac{dH}{dt} = r_H w_t \frac{H\theta_H}{H\theta_H + W\theta_W + w_s} - d_H H - L_{HH} \tag{3}$$

where r_H is the water use efficiency of grass, θ_H and θ_W the rates of water uptake per unit biomass of grasses and trees, respectively, *W* the aboveground woody biomass, d_H the specific loss of grass biomass due to mortality and senescence, and L_{HH} the loss of herbaceous biomass due to grazing. The rate of change of woody biomass over one year can be represented by:

$$\frac{dW}{dt} = r_W w_t \left(\frac{W\theta_W}{H\theta_H + W\theta_W + w_s} + w_s \right) - d_W W - L_{WH} \tag{4}$$

where r_W is the water use efficiency of trees, d_W the specific loss of woody biomass due to mortality and senescence, and L_{WH} the loss of woody biomass due to browsing. Without herbivores, grasses are able to dominate when the amount of infiltrated water is below β (Walker & Noy-Meir 1982). Trees and grasses co-occur when the amount of infiltrated moisture is above this threshold and below the availability at which trees start dominating the vegetation. With increasing moisture availability, the vegetation thus shows transitions from grassland to savanna to woodland (Walker & Noy-Meir 1982, Van Langevelde *et al.* 2003).

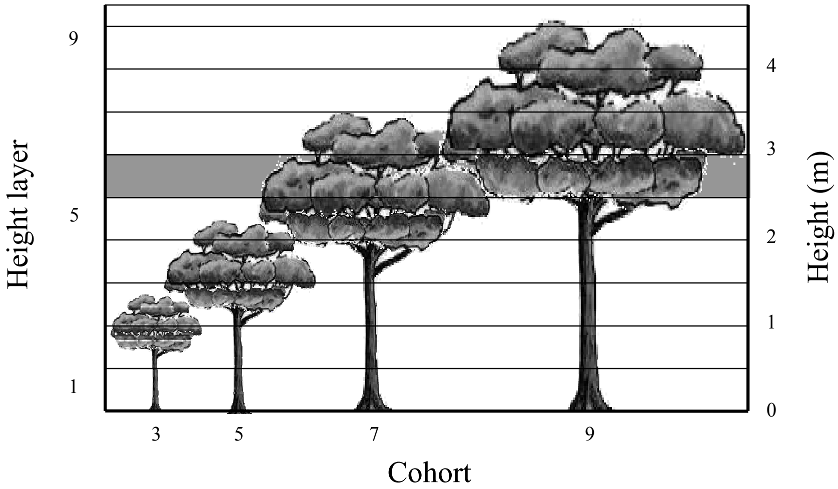


Figure 4.1 Trees of multiple cohorts contributing browse to single height layers, *e.g.*, cohort 7 and 9 both contributing browse to height layer 6 (2.5 – 3.0 m), which is indicated with grey shading.

Since the vertical structure of woody biomass determines the herbivores' access to browse, we expanded the two-dimensional vegetation model as described above with the vertical dimension. For simplicity, our model does not track individual trees, but rather height cohorts of identical individuals. Twenty cohorts (that can co-occur in a single cell) represent the vertical structure of the woody vegetation. A cohort is defined here as a group of individual trees with the same height and other characteristics (*e.g.,* size and shape, all being an allometric function of tree height, Caylor & Shugart 2004). The shortest cohort contains trees of 0.5m in height and subsequent cohorts increase in height with 0.5m height increments up to the tallest cohort of 10m tall trees. Trees of each cohort are characterised by their height (h_t), canopy bottom height (h_b), canopy midpoint height (h_m), canopy width (c_w), total aboveground biomass and a browseable/non-browseable biomass allocation ratio, where large trees have proportionally less browseable biomass than small trees. Browseable biomass is the part of the plant biomass that is eaten by browsers and consists mainly of leaves, but could contain a small proportion of branches. To provide an idealised canopy geometry that closely mimics the shape of a typical savanna tree crown (Caylor & Shugart 2004), canopy width at each layer *d* in the canopy ($c_{w,d}$ with $h_b < d < h_t$) is modelled as:

$$
\begin{aligned}
c_{w,d} &= \sqrt{c_w{}^2\left(1-\frac{(d-h_m)^2}{(h_t-h_m)^2}\right)} && \text{if } d-h_m \geq 0 \\
c_{w,d} &= c_w \exp\left(4\frac{d-h_m}{h_m}\right) && \text{if } d-h_m < 0
\end{aligned}
\qquad (5)
$$

With the total biomass of each cohort in a cell, the browseable biomass is calculated for each cohort and the vertical zonation of all browse in a cell is calculated for height layers with 0.5m increments. Multiple cohorts can thus contribute browseable biomass to a single height layer (Figure 4.1).

Due to growth, a cohort can shift to the next cohort. This increases the total biomass of that cohort, and thus the total woody biomass in the cell. Due to mortality, woody biomass is removed from a cohort, thereby decreasing the total woody biomass in the cell. These two processes, *i.e.,* growth and mortality, are operating simultaneously in each cell, resulting in a change of biomass as calculated with equation (4). The change in biomass is allocated to the different cohorts as a function of the amount of intercepted light per cohort. Growth is modelled to be positively related to the amount of intercepted light per cohort, while for mortality and senescence the relation is negative. Thus, cohorts that intercept a lot of light largely contribute to the increase of woody biomass and experience only small losses. The light intensity at each layer *d* in the canopy (I_d) is calculated using the Lambert-Beer equation:

$$I_d = I_{in} e^{-kW_{b,d+}} \qquad (6)$$

where I_{in} is the incident light intensity above the canopy, *k* is the light extinction coefficient and $W_{b,d+}$ is the total amount of browseable biomass above layer *d* (Huisman *et al.* 1997), assuming that only browseable biomass intercepts light. The amount of intercepted light of cohort *c* (Int_c) is subsequently calculated as:

$$Int_c = \sum_{d=1}^{h_t}\left(I_{in} e^{-kW_{b,d+}}\left(1-e^{-kW_{b,c,d}}\right)\right) \qquad (7)$$

were $W_{b,c,d}$ is the amount of browseable biomass of cohort *c* at layer *d*. Trees in the highest cohort do not grow since they are assumed to have reached their maximum size. Likewise, biomass gain due to the regeneration is kept at a constant proportion of the change in woody biomass as calculated with equation (4). The result will be that without disturbance such as browsing, the woody biomass in a cell grows to the equilibrium standing biomass, consisting exclusively trees in the highest cohort. Browsing can prevent the vegetation from growing to this equilibrium, thereby altering the standing biomass in a cell and its distribution over the cohorts.

Herbivory

The browser and grazer populations are simulated as herds that can distribute freely in the landscape and have complete knowledge regarding the distribution of their food resources. Using an ideal free distribution approach (Fretwel & Lucas 1970) herbivores select cells to forage based on the attractiveness of cells. If several cells have the same attractiveness, the herbivores choose one of the cells at random. Within the yearly simulation loop for plant growth, a foraging loop is implemented. In each step of the foraging loop, the attractiveness of all cells is calculated, and the cell with the highest attractiveness is selected. The herbivores remove λ gram of biomass from the selected cell, and then the next foraging step follows. The foraging loop continues until the requirements of the herbivore population are met and determines L_{HH} (equation 3) and L_{WH} (equation 4) for each cell in the simulated landscape.

Requirements

In the analysis of the effect of herbivory on the vegetation, the population sizes were kept constant. Although it is obvious that a constant population does not hold in large natural systems, we used this assumption because (i) the study was performed on a relatively small area, and more importantly (ii) because we want to isolate the effect of herbivores on vegetation patterning and do not want to include interactive effects of herbivore dynamics. The yearly population food requirement (req_p) is calculated as:

$$req_p = f_d p_{size} \tag{8}$$

where f_d is the yearly food intake as proportion of the body mass of the foragers and p_{size} is the population size in total biomass (Prins & Douglas-Hamilton 1990).

Attractiveness and self facilitation

The effect of the herbivores on landscape heterogeneity depends on the interaction between the pre-existing spatial pattern of the vegetation (Bakker *et al.* 1984; Adler *et al.* 2001) and the spatial pattern of foraging, which is determined by the distribution of the herbivores. Herbivore distribution itself is determined by various factors (*e.g.,* Coughenour 1991, Bailey *et al.* 1996, Hobbs 1996, 1999, Adler *et al.* 2001), but in our model, we confine ourselves to one of its prime determinants: forage. Besides forage availability, forage quality also plays an important role in herbivore distribution; selective foraging occurs in preferred areas. According to optimal foraging theory, animals should forage in a way that maximises the immediate rate of energy gain (Stephens & Krebs 1986). Therefore, the instantaneous energy gain through consuming resources in a cell is taken as measure for the attractiveness of a cell for herbivores. This attractiveness does not only depend on the instantaneous intake rate of food, but also on the digestible energy content of the food (Prins & Olff 1998, Owen-Smith 2002, Drescher *et al.* 2006). We calculate the instantaneous intake rate (I) for both grazers and browsers by means of an asymptotic type II functional response (Holling 1959):

$$I = \frac{i_{\max} F}{g_{½} + F} \tag{9}$$

where i_{max} is the maximum food intake rate at high food abundance, F is the food availability and $g_{½}$ is the food availability at which I reaches half of its maximum (Prins & Olff 1998, Owen-Smith 2002). Only the amount of browseable woody biomass within the physical reach of the browsers is considered as available browse, while the total amount of herbaceous biomass is assumed to be available for the grazers. The instantaneous rate of energy gain from consuming grasses in a cell (E) can be calculated by adding a reduction term for the digestibility of the grasses (Owen-Smith 2002):

$$E = \frac{i_{\max} F}{g_{½} + F} (1-q)^F \tag{10}$$

where q is the reduction term of forage digestibility with increasing grass biomass. Digestibility of grass biomass has been reported to be negatively correlated with standing biomass (Crampton & Harris 1969, Prins & Olff 1998), while the digestibility of browseable material remains constant (Woolnough & Du Toit 2001), although secondary compounds such as tannins increase with leaf age (Du Toit *et al.* 1990). By including a reduction term for grass quality the mechanism for self facilitation for grazers in included in the model. Browsers can not facilitate themselves by improving the quality, but only by increasing the availability of browse that is within reach. The instantaneous rate of energy gain is used as measure of attractiveness of single cells.

Spatially explicit foraging

The distribution of the herbivores does not only depend on the attractiveness of single cells, it may also result from decisions made by the animals at higher spatial scales (Senft *et al.* 1986, Bailey *et al.* 1996). Herbivores are thought to select the landscape unit richest in resources, then the most productive locations within this landscape unit, and so on, down to the most palatable species within a feeding station (Bailey *et al.* 1996). Foraging decisions at broad spatial scales thus can constrain choices at smaller scales (Bailey *et al.* 1996). We therefore calculate the attractiveness of a cell as a weighted average of the attractiveness of all cells in its vicinity using inverse distance weighting:

$$w = dist^{wf} \tag{11}$$

where w is the weighting factor of a cell and wf is the weighting exponent of a cell with distance $dist$ to a cell. In this way, the attractiveness of large-scale landscape units influences the attractiveness of a single cell within this unit.

Herbivory at a certain location also affects the vegetation in neighbouring locations, as the proximity of palatable plants can increase the herbivore damage to both palatable and unpalatable plants in the surroundings (Baraza *et al.* 2006). While foraging in a cell, the herbivores are therefore modelled to also remove a constant fraction (*adj*) of λ from the adjacent cells. In the case of grazing, adjacent cells are only grazed when the standing crop here exceeds the standing crop in the selected cell.

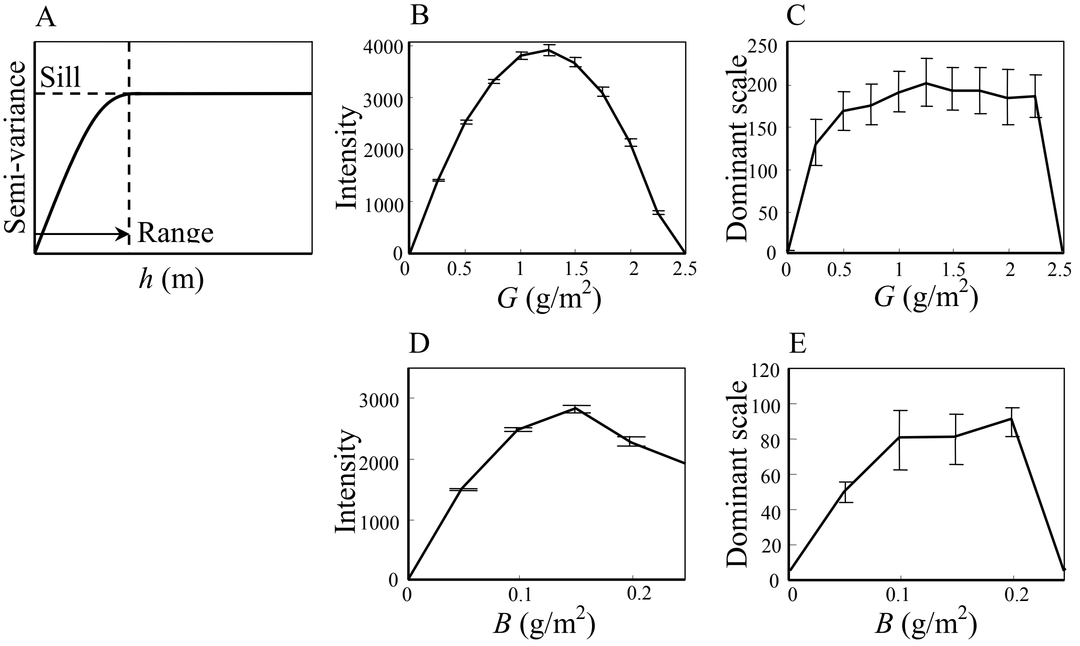


Figure 4.2 Variograms to quantify dominant scale and intensity of the vegetation patterns. Intensity is used as a measure for the variance or heterogeneity, while the dominant scale is a measure for the scale patchiness of the vegetation patterns. We used the variogram to express the degree of spatial variation of grass and woody biomass, as a function of the distance h. (A) The *sill* of the variogram is used to measure the intensity of the landscape thus the semi-variance where the variograms levels off, while the *range* is used as a measure for the dominant scale, *i.e.,* the lag-distance (in meters) where the variogram levels off. (B) Intensity and (C) dominant scale of grass vegetation as function of the grazer density, (D) intensity and (E) dominant scale of the woody biomass as function of browser density. The error bars show 95% confidence intervals of the mean.

Model analyses

Following Murwira & Skidmore (2005), we used variograms to quantify the spatial heterogeneity of the simulated landscapes by quantifying the dominant scale and intensity of these landscapes. Intensity is a measure for the variance in biomass between locations in the landscape, while the dominant scale is a measure for the average vegetation patch size. A variogram is used to express the degree of spatial variation of a regionalised variable, here grass and woody biomass, as a function of distance:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} \left[z(x_i) - z(x_{i+h})\right]^2 \qquad (12)$$

where $\gamma(h)$ is the semi-variance at lag h (*i.e.,* the distance on the ground between sample locations x_i and x_{i+h}), $N(h)$ is the number of observation pairs separated by h, $z(x_i)$ is the value of the regionalised variable at location x_i, and $z(x_{i+h})$ is the value of the regionalised variable at distance h from x_i (Treitz & Howarth 2000). The variance of z between location x_i and x_{i+h} is calculated by sampling in four directions (North to South, East to West, South-West to North-East and North-West to South-East) for each h (Murwira 2003). Following Murwira & Skidmore (2005), the two main structural parameters of the variogram, the sill and the range (Figure 4.2A) are calculated and used to measure respectively the intensity and dominant scale of the vegetation patterns.

Simulations

We simulated model scenarios with variation in parameter values and initial landscapes. We started with simulations where both self facilitation and spatially explicit foraging were systematically introduced into the model to understand their independent effects on spatial pattern formation as well as their interactive effect. Then we performed simulations in which we varied the densities of the browsers and grazers. All of these simulations were performed on initial landscapes which had uniformly distributed amounts of grass and tree biomass in each cell.

Finally, we performed a series of simulations in which we incorporated both different levels of heterogeneity as well as different scales of patchiness. Different levels of heterogeneity in the initial landscapes were obtained by changing the minimum and maximum values between which random values for herbaceous and woody biomass were drawn. We also incorporated different scales of patchiness of the initial landscapes by grouping cells together in a checkerboard style and assigning them the same random value for herbaceous and woody biomass.

Results

If we analyse the model without herbivores, the resultant standing biomass of trees and grasses in each grid cell is only determined by the amount of infiltrated water and the soil characteristics. Since we kept the amount of infiltrated water and soil characteristics equal for all cells and constant during the simulations, every cell is identical to the others resulting in homogeneous vegetation without patterns, regardless of the initial landscape conditions. The tree layer then consists exclusively of trees in the highest cohorts, because there are no disturbances that prevent the trees from growing tall.

Conditions for herbivores to create vegetation patterns

Figure 4.3 shows the interactive effect of self facilitation and spatial dependence of foraging on the formation of vegetation patterns. Without self facilitation, the herbivores create a landscape with only small-scale cell-to-cell heterogeneity, but without large-scale vegetation patterns

(Figure 4.3). With self facilitation, but without spatial dependence of foraging, the resultant landscape shows only small-scale vegetation patterns due to selective foraging in preferred cells (Figure 4.3). Moreover, when including spatial dependence, vegetation patterns are only created if the weight of neighbouring cells in determining attractiveness is high. When including both factors simultaneously, the effect of the herbivores on spatial vegetation patterns is amplified and hence the scale of the vegetation patterns is increased (Figure 3.4A). When the amount of forage consumed in adjacent cells or the weighting of surrounding cells in the assessment of a cell's attractiveness increases, the scale of the vegetation patterns increases (Figure 4.3B).

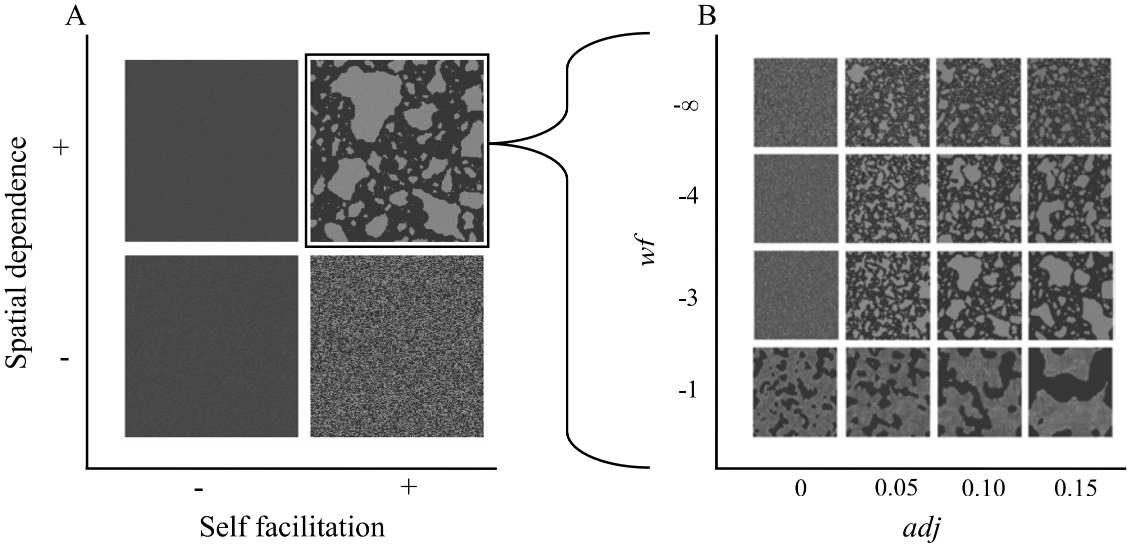


Figure 4.3 (A) Vegetation patterning in relation to the two driving mechanisms: spatial dependence of foraging and self facilitation, where – means that the assumption is not included in the model, and + means that the assumption is included in the model. (B) Spatial dependence of foraging split up in adj (the fraction foraged in adjacent cells relative to the selected cell) and wf (the weighting factor of cells in the neighbourhood of a cell). Grey tone represents the amount of grass biomass, with dark grey expressing a high biomass, and light grey a low biomass. Each landscape comprises 200x200 cells of 5x5m each.

Changing grazer density

In a landscape with a high standing biomass, grazers increase the attractiveness of grazed cells and these cells will consequently be visited repeatedly as long as regrowth of the grass is faster than the time within which grazers return. Since the grazers also forage in cells adjacent to the selected cell, they also increase the attractiveness of these adjacent cells. At low grazing pressure, the grazers therefore create small grazed patches (Figure 4.4). With increasing grazing pressure, the grazed patches become larger, will merge, and form one large patch. When the grazing pressure increases even more, the grazers exploit the entire landscape and the overall grass biomass drops below the optimal standing biomass. As a result, the intensity and dominant scale of the vegetation show a hump-shaped response to increasing grazing pressure (Figure 4.2B and 4.2C respectively). Grazers can thus create large-scale vegetation patterns in our model, with the type of pattern depending on the density of the grazer population.

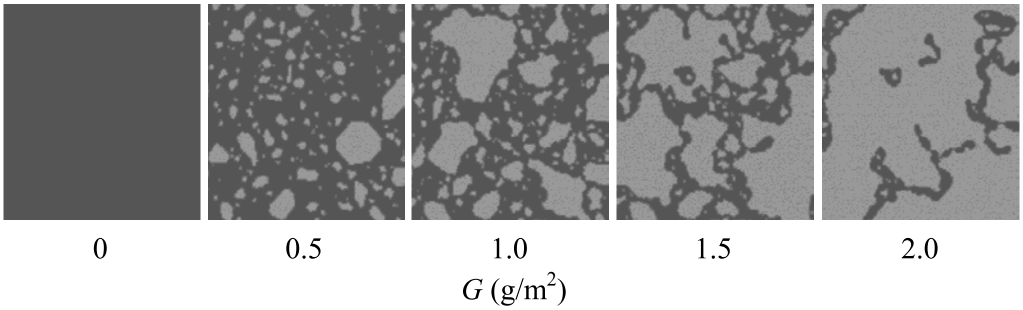


Figure 4.4 Vegetation patterning as a function of grazer density (G). Grey tone represents the amount of grass biomass, with dark grey expressing a high biomass, and light grey a low biomass. Each landscape comprises 200x200 cells of 5x5m each.

Changing browser density

In contrast to grazers, browsers do not experience a decline in forage quality with increasing standing woody biomass. However, because of the vertical structure of the woody vegetation browsers select cells with the highest amount of browseable biomass that is within reach of the browsers to forage. Although browsing results in a decrease of the amount of forage in the short term, the amount of accessible browse remains high relative to a situation without browsers (Figure 4.5) in the long term. Hence, browsers are able to facilitate themselves by increasing the amount of available forage. The resultant landscapes with browsers therefore consists of browsed patches, where the woody biomass is being suppressed

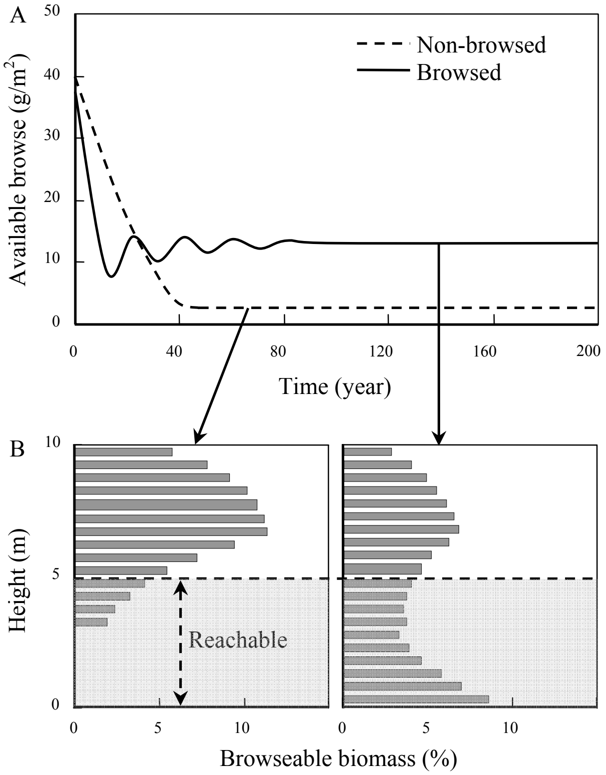


Figure 4.5 (A) The dynamics of reachable browseable biomass (*i.e.*, browse between 0-5m high) in a cell without spatially explicit browsing: the amount of browseable woody biomass without (dotted line) and with browsing (continuous line). (B) Vertical distribution of browseable biomass with and without browsing after simulating 200 year. Browsing thus enhances the amount of available browse.

by the browsers and the trees are kept small, and unutilised patches, where the trees are able to grow to full size. With increasing browser density, the browsed patches grow in size until browsers use almost the entire woody vegetation, with only scattered areas of unbrowsed vegetation (Figure 4.6). When browser density increases even more, they are able to suppress the entire woody vegetation, creating spatially homogeneous vegetation at a large scale, with only small-scale patches due to differences in biomass removal from selected and adjacent cells (Figure 4.2D). The dominant scale shows a hump-shaped response to browser density. This shows that browsers are able to create vegetation patterns, with the type and scale of pattern being dependent on their density.

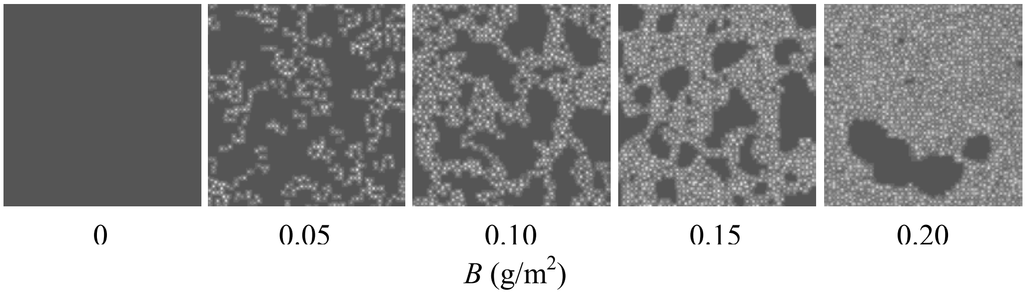


Figure 4.6 Vegetation patterning as a function of browser density (*B*). Grey tone represents the amount of woody biomass, with dark grey expressing a high biomass, and light grey a low biomass. Each landscape comprises 200x200 cells of 5x5m each.

Interactions with pre-existing vegetation patterns

If we now analyse the model for different initial landscape configurations, we see that both the heterogeneity of the initial vegetation as well as the scale of patchiness of the pre-existing vegetation patterns do influence the vegetation patterns as produced by the herbivores (Figure 4.7).With increasing heterogeneity of the initial landscape, the scale of the resultant vegetation patterns decreases. On the other hand, the scale of the resultant vegetation patterns also increases when the scale of patchiness of the initial vegetation increases. According to our model, the initial landscape configuration becomes more important in determining the resultant vegetation patterns when the initial heterogeneity or patchiness of the vegetation is larger.

Discussion

In this paper, we address the question through which mechanisms herbivores can induce vegetation patterns in savannas, and how the role of herbivory as a determinant of vegetation patterning changes with different pre-existing vegetation patterns. To answer these questions, we developed a spatially explicit simulation model, including growth of grasses and trees, vertical zonation of browseable biomass, and spatially explicit foraging by grazers and browsers. The trends produced by the model show that the formation of spatial vegetation patterns in savannas due to herbivory depends on the interaction between two mechanisms, namely self facilitation by the herbivores and spatially explicit foraging. This means that (i) there has to be a reason for herbivores to revisit a site, *e.g.,* through an increased availability or quality of forage, and (ii) foraging at a site should influence vegetation at larger spatial scales.

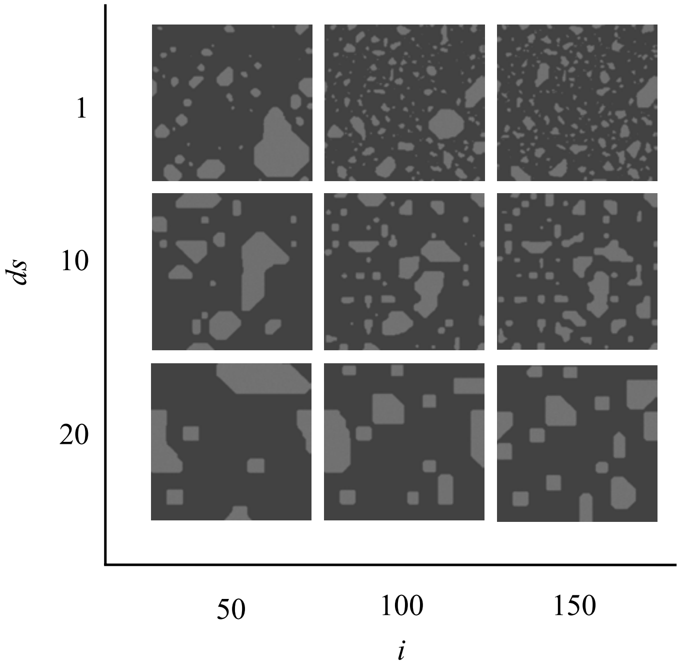


Figure 4.7 Vegetation patterns after simulations with grazers included and variation of the heterogeneity and patchiness of the initial vegetation. *ds* represents the dominant scale of patchiness of the initial landscape, computed as a chessboard-like initial landscape where *ds*ds* cells are all assigned the same (random) value of grass biomass. *i* represents the heterogeneity of the initial landscape, here computed as the interval (280 ± *i*) out of which random values are drawn to be assigned to each cell or group of cells.

Self facilitation can emerge from increasing the nutritional quality of vegetation or increasing the amount of available forage while foraging. In our model, the first case applies to the grazers, while the latter one is applicable to the browsers. Adler *et al.* (2001) argues that feedbacks between grazing and plant quality may be important sources of spatial patterning since they promote the continued use of previously grazed patches. These feedbacks include increased nutritional content of the forage material (Coppock *et al.* 1983, McNaughton 1984, Du Toit *et al.* 1990, Jefferies *et al.* 1994), a reduction in senescent material and maintenance of leaves in an early phenological state (Richards *et al.* 1962, Hobbs 1999). The positive effect of repeated grazing on forage quality, however, can decline in the long term, when grazing remains intensive and it leads to a change in plant species composition to less palatable species (Coppock *et al.* 1983). As we did not take plant species composition into account, the predicted spatial patterns could not reproduce this reversing effect. The vegetation patterns of grass biomass as produced by our model are similar to the vegetation patterns that Cid & Brizuela (1998) found as result of grazing by Aberdeen Angus steer on initially homogeneous fescue paddocks. They showed that, within one season, cattle revisited some sites within the paddocks more often while neglecting other sites. This resulted in a mosaic of heavily utilised and lightly utilised patches. Heavily utilised patches in their study had lower biomass values than the lightly utilised patches. In contrast to grazing, browsing increases the amount of browse within reach of the herbivores. High browsing pressure can prevent the establishment of woody seedlings and retard the growth of shrubs, suppressing their recruitment into the mature stage (Pellew 1987, Prins & Van der Jeugd 1993, Roques *et al.* 2001, Augustine & McNaughton 2004, Fornara & Du Toit 2007). In this way, patches with high trees emerge when browsers are not able to suppress the entire woody vegetation.

However, we claim that self facilitation alone is not sufficient to produce spatial vegetation patterning. Spatially explicit foraging is necessary to induce patterning. We modelled this by including the attractiveness of a cell's environment in the assessment of the attractiveness of the particular cell, and by foraging in cells adjacent to selected cells. The first case can be interpreted as hierarchical foraging decisions (*e.g.,* Senft *et al.* 1986, Bailey *et al.* 1996), where herbivores make decisions at different spatial-temporal scales and where large-scale decisions influence decisions at smaller scales. The herbivore pressure at a certain location also results in consuming the vegetation at neighbouring locations, as the proximity of palatable plants can increase the herbivore damage to both palatable and unpalatable plants in the surroundings (Baraza *et al.* 2006). This effect of foraging at neighbouring locations is small when the central location attracts few herbivores, and it decreases with increasing distance from the central location to which the herbivores are attracted.

Our model analyses show that at intermediate herbivore densities, the intensity and dominant scale of the resultant vegetation patterns increase. With higher herbivore densities, the herbivores are forced to be less selective, and hence the level of heterogeneity and patchiness of the vegetation decreases. These findings are consistent with the predictions from Adler *et al.* (2001) that the heterogeneity of vegetation decreases when herbivory is distributed spatially more homogeneous. The model also shows that the pre-existing pattern of vegetation increasingly influences vegetation patterning due to herbivory when the heterogeneity and patchiness of the initial landscape increases. Adler *et al.* (2001) postulate that when grazing is a dependent function of the pre-existing vegetation pattern (termed "selective grazing" in their paper), then patterns emerge only if grazing positively influences the resource levels of grazed patches (*i.e.*, self facilitation), and otherwise patterns will disappear. We also generate this hypothesis as only through the inclusion of self facilitation spatial vegetation patterns could be produced (Figure 4.6). Additionally, we show that the influence of the pre-existing vegetation in determining vegetation patterning through herbivory decreases when the initial heterogeneity and scale of patchiness of the initial vegetation is smaller. Conversely, herbivores are predicted to conform their consumption pattern more to patterns in the initial vegetation when the patterns in the initial landscape are more pronounced. Hence, the level of adherence of the herbivores to forage in pre-existing patches increases when these pre-existing patches increase in size and when the level of heterogeneity in vegetation increases.

We can conclude that herbivores can induce vegetation patterning in savannas when herbivores increase the attractiveness of a location for foraging and foraging is spatially explicit. When both conditions are satisfied, the resultant vegetation patterns depend however on the pre-existing pattern in vegetation. The influence of the pre-existing vegetation patterns on the role of herbivory declines when the heterogeneity and patchiness of the pre-existing vegetation is smaller. Furthermore, herbivores only generate spatial vegetation patterns at low to intermediate densities. These findings, and critical experimentation of their ecological validity, will increase our understanding of heterogeneity and vegetation patterning, and the role of plant-herbivore interactions therein.

CHAPTER 5

Spatial patterns in savanna trees and grasses due to herbivory

JACOB C. DOUMA, FRANK VAN LANGEVELDE, THOMAS A. GROEN, CLAUDIUS A.D.M. VAN DE VIJVER & HERBERT H.T. PRINS

Abstract

In savannas, trees and grasses co-occur in different spatial patterns over a range of environmental conditions. However, a general mechanism is lacking which can alternatively explain the spatial patterning of trees and grasses in savannas over a range of environmental conditions. Using a spatially explicit model, we show that patterning of savanna trees and grasses can be explained by resource competition between trees and grasses and herbivory, *i.e.*, grazing and browsing, where herbivore pressure at a certain location also has an effect on the vegetation in neighbouring locations. Our model includes the dynamics of herbaceous and woody biomass and changes in local grazing and browsing pressure. The resulting vegetation patterns are self-organising because regular patterns in trees and grasses occur, regardless initial conditions. We found that patterns in vegetation can emerge under different environmental conditions (*i.e.*, gradients of soil water or nutrient availability), when consumers that are attracted to high plant biomass of the superior competitor facilitate growth of the inferior competitor in the surroundings. Whereas former studies argue that patterns in vegetation emerge as result of small-scale facilitation and large-scale competition, we found that patterns can be explained by local competition between trees and grasses and large-scale facilitation by herbivory. With this finding, our study contributes to the growing body of evidence for common mechanisms for pattern formation in biological systems.

Keywords: *browsing, grazing, savanna ecology, scale-dependent feedback, tree-grass dynamics.*

Introduction

Savannas are characterized by the co-occurrence of trees and grasses over a range of environmental conditions (Scholes & Archer 1997, Sankaran *et al.* 2005) in different spatial patterns (Okali *et al.* 1973, Archer *et al.* 1988, Archer 1990, Menaut *et al.* 1990, Ponce & Da Cunha 1993, Couteron 2002, Lejeune *et al.* 2002, Scholes *et al.* 2002, Breshears 2006, Figure 5.1). A complex set of interacting factors, *i.e.*, fire, herbivory, soil type and rainfall, determines the relative abundance and spatial patterning of trees and grasses (Scholes & Archer 1997, Van Langevelde *et al.* 2003, Sankaran *et al.* 2004, 2005). For the spatial patterning of savanna trees and grasses, several explanations have been proposed, ranging from small-scale heterogeneities like seed clumping, clonal growth, improved local moisture conditions or vegetation clearing (Jeltsch *et al.* 1996, 1997, 1998, Van Wijk & Rodriguez-Iturbe 2002), to nutrient redistribution (Lejeune *et al.* 2002), tree clustering (Archer *et al.* 1988, 1989, 1990), facilitation of palatable plants under the protection of unpalatable plants (Olff *et al.* 1999), and patterns in substrate and topography. These explanations might be responsible for patterns under certain conditions. However, a general mechanism is lacking which can alternatively explain the spatial patterning of trees and grasses in savannas over a range of environmental conditions.

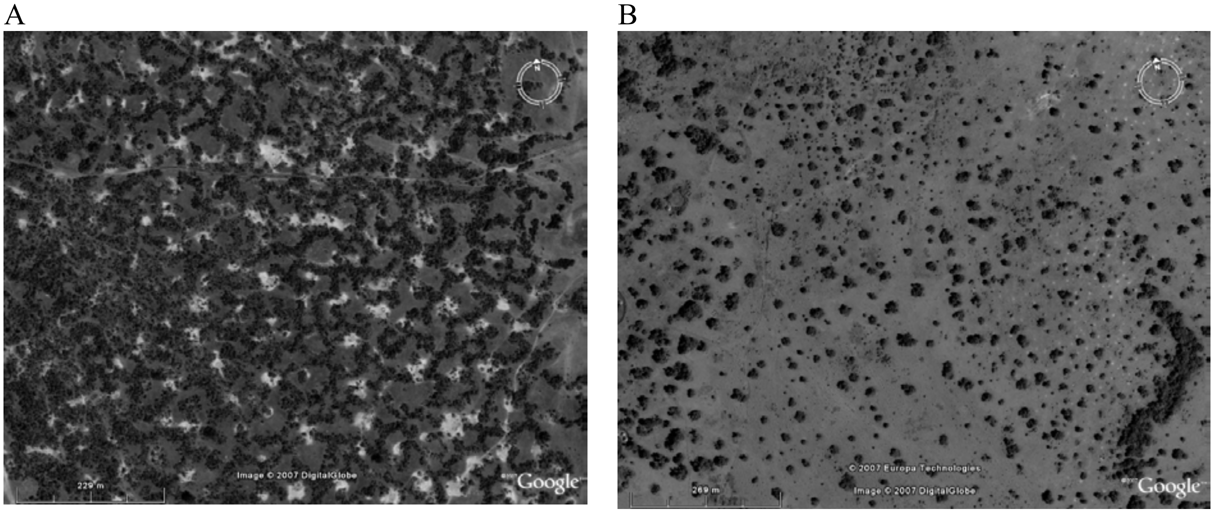


Figure 5.1 Patterns in savanna trees and grasses (A) labyrinth patterns in Mali (13°03’13.21” N, 6°40’53.36” W, elevation 325 m ASL, eye altitude 1.12 km ASL), and (B) spots in Kenya (1°17’35.47” S, 34°56’58.25” E, elevation 1920 m ASL, eye altitude 2.85 km ASL) (using Google Earth™)

Recently, vegetation patterning is explained as self-organising (Klausmeier 1999, Rietkerk *et al.* 2002, 2004) because patterns are regular, regardless of initial model conditions. Vegetation patterns resulting from this self-organisation are observed in many ecosystems throughout the world (see Rietkerk *et al.* 2004 for an overview). One mechanism to explain the variety, in both scale and shape, of patterns observed in arid regions, is the positive feedback between plant density and water infiltration (Ludwig *et al.* 1999, HilleRisLambers *et al.* 2001, Rietkerk *et al.* 2002, 2004, Lejeune *et al.* 2004, Meron *et al.* 2004). Models based on this positive feedback produce a set of different patterns, *e.g.*, vegetation bands, labyrinths and spots in the herbaceous vegetation. Lejeune *et al.* (2002) propose a mechanism for the formation of wooded patches based on redistribution of nutrients. However, as only a small range of savanna systems is nutrient limited for plant growth (Scholes & Archer 1997) and the positive feedback between plant density and water infiltration is mainly expected under arid conditions (Rietkerk *et al.* 2004), the redistribution of nutrients and water is not likely to be a general mechanism to explain pattern in savanna trees and grasses over a range of rainfall and soil types.

In this paper, we investigate whether patterning in savanna trees and grasses can be explained by herbivory and competition for a shared resource between trees and grasses. Generally, trees and grasses compete for a limiting resource, which could be water at a certain location and moment in time (Scholes & Archer 1997, Schenk & Jackson 2002), or nutrients (Lejeune *et al.* 2002, Loth *et al.* 2005) or light (Ludwig *et al.* 2004) at other locations or moments. In this paper, we assume that one resource is limiting for tree and grass growth without further specifying which resource. Browsing and grazing also largely influence the ratio of trees and grasses in nearly all savanna regions worldwide. Browsers reduce woody biomass, limit tree recruitment (Prins & Van der Jeugd 1993) or push over trees (Van de Vijver *et al.* 1999). Grazers reduce grass biomass and decrease the effect that fire has on trees and shrubs, because grass biomass provides fuel for fire and fire intensity is largely determined by this fuel load (Shea *et al.* 1996, Van Langevelde *et al.* 2003). The aim of our paper is to explain spatial patterning of trees and grasses under different levels of resource supply rate, differences in competition strength between trees and grasses, and different levels of browsing and grazing. Therefore, we developed a spatially explicit model for savanna trees and grasses and investigated the conditions for pattern formation.

Model

Our model describes changes in biomass of trees and shrubs (W) and grasses (H) in space and time. Trees and grasses compete for the same resource and have a direct as well as indirect negative effect on each other. The direct effect is through the competition for light, water or nutrients. The indirect effect operates via the negative effect of grasses on trees through fire (Van Langevelde *et al*. 2003). Fire either kills trees or reduces their size, the degree in which this occurs depends, among others, on fuel load. Grasses themselves are less susceptible to fire damage as they generally burn when in senescence and recovery is rapid (within one to a few growing seasons, Van de Vijver *et al.* 1999).

Another important factor influencing tree-grass dynamics is herbivory. Browsers (B) and grazers (G) are able to remove large amounts of woody and grass biomass, respectively. As browsers consume leaves and twigs and push over trees, the competitive effect of trees on grasses will decrease due to browsing. This decrease consequently results in an increase of grass growth (Prins & Van der Jeugd 1993, Van de Koppel & Prins 1998). Similarly, increasing grazing pressure will provide opportunities for trees to increase in cover and biomass as the effects of fire decrease and grass uses fewer resources, resulting in higher resource availability for trees. In savannas with high livestock pressure, dramatic increases in tree cover due to high levels of grazing have been described numerously and are often referred to as bush encroachment (Roques *et al.* 2001, Briggs *et al.* 2002). To model these relationships, we assume that tree and grass growth depends on the resource supply rate (r), resource holding capacity of the soil (μ) and the resource use efficiency of the plants ($e_\bullet$). Model parameters and variables are listed in Table 5.1. The values of these parameters were based on realistic values from literature when possible, while others were calibrated to make the model run within realistic bounds.

Several formulations exist to describe plant growth, for example, a constant per capita rate of growth, density dependent growth (*e.g.*, logistic growth), or taking into account a (below-ground) reserve that is not accessible to herbivores. To allow for an analytical model analysis, we adopt a formulation where plant growth decreases monotonically with increasing plant biomass. Furthermore, the growth rate of the one growth form is inversely related to the density of the other.

We modelled the growth rate for grasses as

$$r e_H \, \mu \frac{k_H}{k_H + f(W)W} \tag{1}$$

This function assumes plant growth to be maximal at low plant biomass. It is a very simplistic description of plant growth, assuming an unlimited below-ground reserve. In the function of the grass growth rate, we further assume a density dependent competitive effect of trees on grasses that increases with increasing woody biomass. The competitive effect is assumed to be almost absent at low woody biomass, while competition becomes severe at higher woody biomass. Some studies indeed suggest that the negative effect of the one growth form on the other becomes significant when a certain biomass is reached (Scholes & Archer 1997). This non-linear increase of the competitive effect is represented by the function $f(W)$, for which we used $f(W) = \beta W$, where β is the coefficient determining the strength of the density dependent competitive effect of trees on grasses. A high value for β means that the inhibiting effect of trees on grasses is especially high at high tree biomass. The parameter k_H is the half saturation constant at which value the effect of trees on grasses is half of its maximum. The function for the growth rate of trees is similarly formulated as equation 1.

Table 5.1 List of model parameters and variables, their units and values.

	Interpretation	Units	Values
H	Grass biomass	g m^{-2}	
W	Tree biomass	g m^{-2}	
B	Browser density	g m^{-2}	
G	Grazer density	g m^{-2}	
R	Resource supply rate	mm d^{-1}	0-25
μ	Resource holding capacity of the soil	[-]	0.2
e_W	Resource use efficiency of trees	g m^{-2} mm^{-1}	0.005-0.6
e_H	Resource use efficiency of grasses	g m^{-2} mm^{-1}	0.2
c_B	Biomass loss of trees due to consumption	m^2 g^{-1}d^{-1}	0.01
c_G	Biomass loss of grasses due to consumption	m^2 g^{-1}d^{-1}	0.01
g_B	Conversion coefficient of woody biomass into browser biomass	[-]	0.05
g_G	Conversion coefficient of grass biomass into grazer biomass	[-]	0.05
m_W	Loss rate of trees due to senescence	d^{-1}	0.002
m_H	Loss rate of grasses due to senescence	d^{-1}	0.002
m_B	Fraction of the browser density leaving each time step	d^{-1}	0.01
m_G	Fraction of the grazer density leaving each time step	d^{-1}	0.01
k_W	Coefficient determining shape of competition function of trees	g^2 m^{-4}	10
k_H	Coefficient determining shape of competition function of grasses	g^2 m^{-4}	10
α	Coefficient determining the strength of the density dependent effect of grasses on trees	[-]	0.05-20
β	Coefficient determining the strength of the density dependent effect of trees on grasses	[-]	1
D_W	Diffusion coefficient for trees	m^2 d^{-1}	0.005
D_H	Diffusion coefficient for grasses	m^2 d^{-1}	0.005
D_B	Diffusion coefficient for grazers	m^2 d^{-1}	0.4
D_G	Diffusion coefficient for browsers	m^2 d^{-1}	0.4
x, y	x and y location of modelled area	m	200
T	Time	d	8000

Loss of biomass of trees and grasses is due to senescence and herbivory. We modelled senescence as a fixed fraction of the present biomass ($m_\bullet$). Loss due to herbivory depends on the local herbivore pressure and their intake rate ($c_\bullet$). The spread of the vegetation is represented by a two-dimensional diffusion equation and depends on the diffusion coefficient ($D_\bullet$). The change in biomass of trees and grasses is, therefore, represented by the two partial differential equations

$$\frac{\partial W}{\partial t} = r\, e_W\, \mu \frac{k_W}{k_W + \alpha H^2} - c_B\, B W - m_W\, W + D_W \left(\frac{\partial^2 W}{\partial x^2} + \frac{\partial^2 W}{\partial y^2} \right) \tag{2}$$

$$\frac{\partial H}{\partial t} = r\, e_H\, \mu \frac{k_H}{k_H + \beta W^2} - c_G\, G H - m_H\, H + D_H \left(\frac{\partial^2 H}{\partial x^2} + \frac{\partial^2 H}{\partial y^2} \right) \tag{3}$$

We modelled the changes in herbivory pressure at a certain location as the difference between the increase and decrease of herbivore density at this location. We assume an open system where herbivores can aggregate or leave depending on the local attraction of the vegetation as forage. The increase in local browser density is related to the gain browsers can realise on this location, based on the local woody biomass (W), the intake rate of the browsers (c_B) and the conversion coefficient of woody biomass into browser biomass (g_B). The decrease in local browser density is set as a fraction leaving the location each time step (m_B). The herbivore pressure at a certain location also results in consuming the vegetation at neighbouring locations, as the proximity of palatable plants can increase the herbivore damage to both palatable and unpalatable plants in the surroundings (Baraza *et al.* 2006, Smit *et al.* 2007). This effect of foraging at neighbouring locations is small when the central location attracts few herbivores, and it decreases with increasing distance from the central location to which the herbivores are attracted. To keep the model analytically tractable, we modelled this foraging at surrounding locations using a two-dimensional diffusion equation to account for the decreasing herbivore pressure further away from the central location. The change in local herbivore density of browsers and grazers is formulated as

$$\frac{\partial B}{\partial t} = B\left(c_B\, g_B\, W - m_B\right) + D_B \left(\frac{\partial^2 B}{\partial x^2} + \frac{\partial^2 B}{\partial y^2} \right) \tag{4}$$

$$\frac{\partial G}{\partial t} = G\left(c_G\, g_G\, H - m_G\right) + D_G \left(\frac{\partial^2 G}{\partial x^2} + \frac{\partial^2 G}{\partial y^2} \right) \tag{5}$$

where $D_\bullet$ is the speed with which animals move to neighbouring locations while foraging. Note that we do not model changes in overall herbivore population size, but local herbivore pressure. We assume that the grazers and browsers range freely but that foraging is spatial dependent as consuming at a certain location and its surroundings.

Results

Analysis of the non-spatial model

First, we analysed the model without any spatial component (*i.e.*, without the diffusion equations) to investigate the stability conditions of the state variables (where the change in W, H, B and $G = 0$). To investigate the stability conditions, equations 2-5 were solved analytically. Three relevant solutions exist, namely an internal equilibrium and two boundary equilibria. When the internal equilibrium is stable, the system contains trees, grasses, browsers and grazers. In boundary equilibrium 1, there is a stable system without grazer pressure and trees are dominant, whereas browser pressure is absent and grasses are dominant in boundary equilibrium 2. In Appendix 5.1, these equilibria and the formal stability analyses are presented.

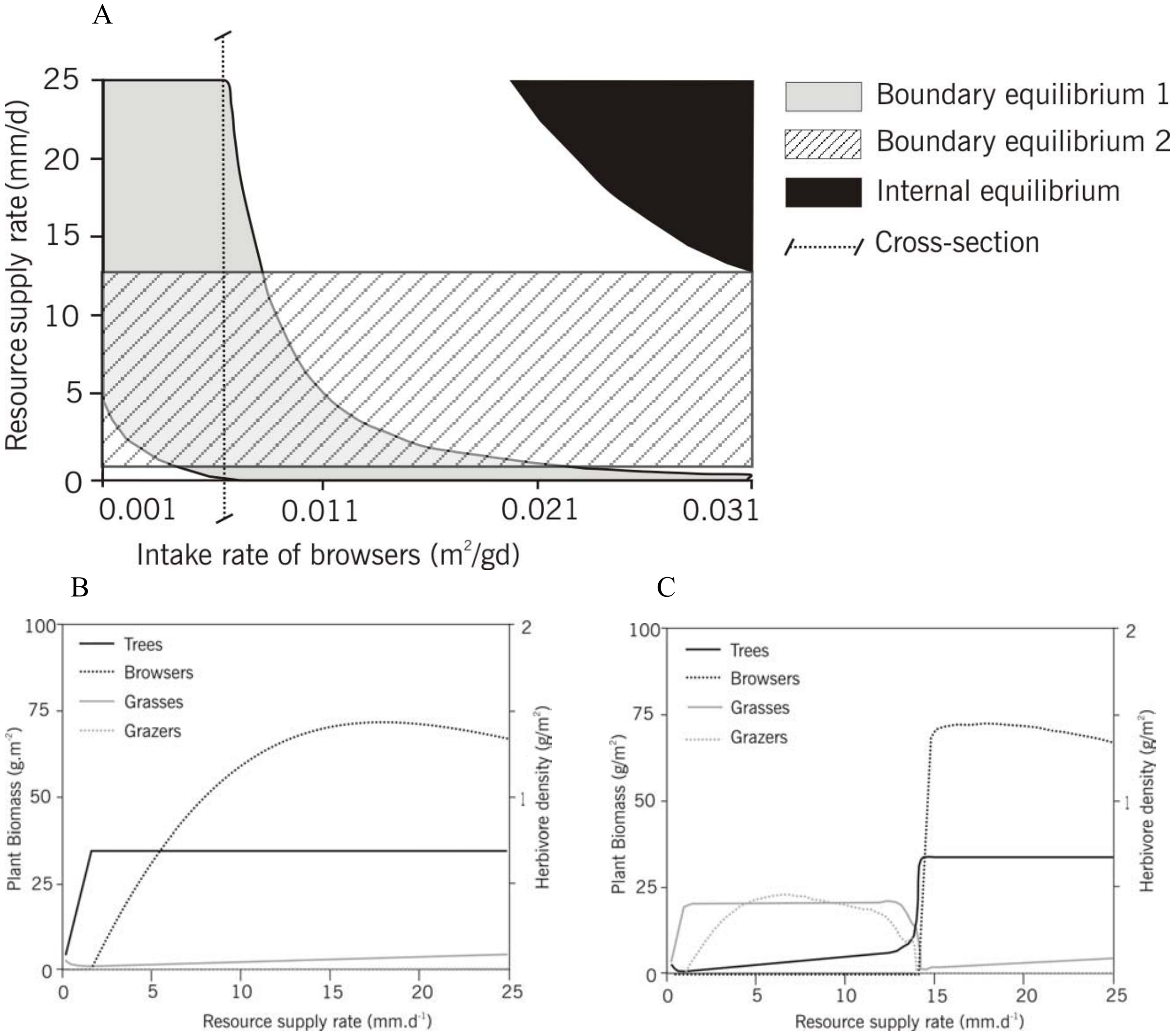


Figure 5.2 (A) Parameter plane of the intake rate of the browsers (c_B) and the resource supply rate (r) showing three possible stable equilibria of the non-spatial model, namely the internal equilibrium and two boundary equilibria. In boundary equilibrium 1, there is a stable system without grazers and dominance of trees. In boundary equilibrium 2, there is a stable system in which grasses are dominant and no browsers are present. For some parameter values, the two boundary equilibria co-occur. In this parameter region, tree or grass dominance is strongly dependent on the initial conditions. Given are these boundary equilibria 1 (B) and 2 (C) of woody and grass biomass and grazer and browser density along the cross-section indicated in Figure 5.2a. Parameter values: $e_W = 0.2$, $e_H = 0.2$, $\mu = 0.2$, $k_W = 10$, $k_H = 10$, $c_G = 0.01$, $m_W = 0.002$, $m_H = 0.002$, $g_B = 0.05$, $g_G = 0.05$, $m_B = 0.01$, $m_G = 0.01$, $\alpha = 1$, $\beta = 1$. See Table 5.1 for parameter descriptions.

Figure 5.2A shows under which values of the intake rate of the browsers (c_B) and resource supply rate (r) the three equilibria are stable. The varying intake rates of the browsers can be interpreted as the effect that different browser species can have on the vegetation. The internal equilibrium is stable but oscillates over time. For some parameter values, the two boundary equilibria co-occur. In this parameter region, the savanna system can be either tree or grass dominated, strongly depending on the initial conditions. If the initial conditions are close to the equilibrium values of boundary equilibrium 1, it is likely that the system becomes tree dominated (Figure 5.2B). The same is true for boundary equilibrium 2, resulting in the dominance of grasses (Figure 5.2C). In both boundary equilibria, trees and grasses are present, but which the dominant growth form differs. The model allows that both trees and grasses co-occur, although one growth form has low biomass levels. With increasing resource supply rate, plant biomass increases until the consumers regulate the vegetation. With increasing intake of the browsers, trees become less and less dominant. At lower levels of the resource supply rate, browser pressure is lower due to less woody biomass, and the region where trees are dominant is larger. Note that in Figure 5.2, the parameter values for trees and grasses are similar. We do not consider yet the situation where the one growth form is competitively superior.

Analysis of the spatial model

For spatial pattern formation, the non-spatial equilibrium of trees and grasses has to be stable and the spatial equilibrium should be unstable. These two criteria are indicative for the principle of pattern formation as first outlined by Turing (1952). If the system is subject to spatially homogeneous perturbations, the system will return to its original equilibrium again. However, if a spatially heterogeneous perturbation is introduced in the system, it will not return to its original state. Due to this perturbation, a local small increase of the one growth form will lead to a further biomass increase due to growth, and simultaneously suppressing the other growth form by competition. Therefore, the system locally deviates from the original equilibrium and will turn to a new stable equilibrium. With these two criteria, it is possible to determine the regions of pattern formation as function of resource supply rate (r) and browser intake rate (c_B, Figure 5.3). We still consider trees and grasses to be similar in terms of parameter values. For the formal Turing analysis, see Appendix 5.2.

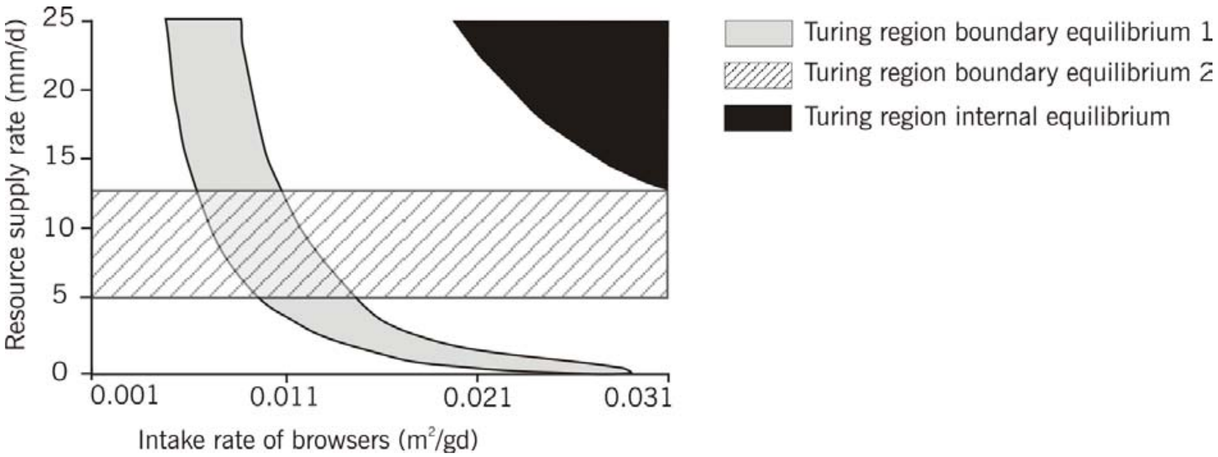


Figure 5.2 Parameter plane of the intake rate of the browsers (c_B) and the resource supply rate (r) showing under which parameter conditions pattern formation can occur in the spatial model. Parameter values are: $e_W = 0.2$, $e_H = 0.2$, $\mu = 0.2$, $k_W = 10$, $k_H = 10$, $c_G = 0.01$, $m_W = 0.002$, $m_H = 0.002$, $g_B = 0.05$, $g_G = 0.05$, $m_B = 0.01$, $m_G = 0.01$, $\alpha = 1$, $\beta = 1$, $D_W = 0.005$, $D_H = 0.005$, $D_B = 0.4$, $D_G = 0.4$, $Q = 0.3$. See Table 5.1 for parameter descriptions.

We simulated the model to analyse the resulting spatial patterns using a forward Euler integration method with zero flux boundaries. A spatial grid of 200×200 cells with size of 2.5×2.5 m was set up. In the simulations, we randomly started with the presence of trees, grasses, browser and grazer pressure in 50% of the cells, whereas the other 50% of the cells were empty. Different pattern types are produced with changing intake rate of the browsers (c_B) and with increasing resource supply rate (r). At low values for c_B, trees are dominating (Figure 5.4). With increasing values for c_B, gaps in woody cover are formed, changing into labyrinths to spots. The change in pattern type with increasing intake rate of the browsers can be explained by increased browser pressure. With high intake rate, browsers remove more woody biomass, leading to a reduced competitive effect of the trees on grasses, resulting in increasing grass growth. Increased resource supply rate leads to denser patterns, because plant biomass production increases.

As can be seen in Figure 5.4, the parameter region in which patterns are observed is larger than predicted by the Turing analysis (Figure 5.3). Rietkerk *et al.* (2002) also found pattern formation outside the parameter region where the Turing analysis predicts patterns. In Figure 5.4A and Figure 5.4B, different initial conditions were chosen, with the same resource supply rate and intake rate gradient resulting in different parameter regions with patterns. In general, it can be concluded that depending on the initial values chosen either the domain of boundary equilibrium 1 or 2 is entered. These initial values determine the dominance of either trees or grasses for certain parameter values. For example, when we start with a tree-dominated savanna with low resource supply rate and browser intake rate, grasses are not able to invade and outcompete woody biomass and trees remain dominant (Figure 5.4A). Likewise, in a grass-dominated savanna, trees are not able to invade the grassland, despite the low intake rate of the browsers (Figure 5.4B).

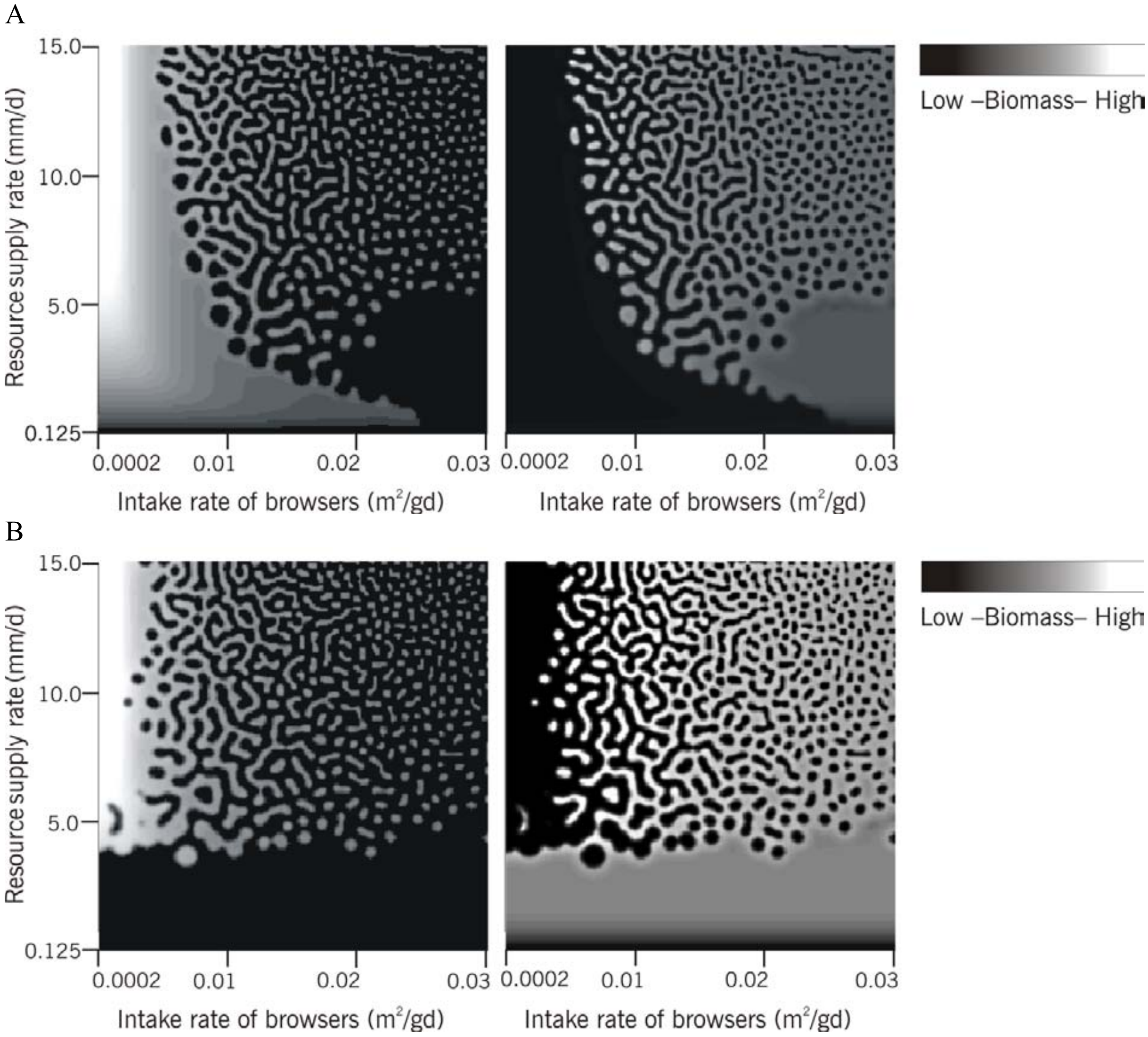


Figure 5.4 Spatial patterns of trees (left) and grasses (right) for increasing intake rate of the browsers (c_B) along the x-axis and increasing resource supply rate (r) along the y-axis after 8000 d based on (A) boundary equilibrium 1 and (B) boundary equilibrium 2. The simulations cover a spatial grid of 200×200 cells with size of 2.5×2.5m. Initial values are: (a) $W = 20$, $H = 10$, $G = B = 0.4$, and (b) $W = 1$, $H = 20$, $G = B = 0.4$. Other parameters are: $e_W = 0.2$, $e_H = 0.2$, $\mu = 0.2$, $k_W = 10$, $k_H = 10$, $c_G = 0.01$, $m_W = 0.002$, $m_H = 0.002$, $g_B = 0.05$, $g_G = 0.05$, $m_B = 0.01$, $m_G = 0.01$, $\alpha = 1$, $\beta = 1$, $D_W = 0.005$, $D_H = 0.005$, $D_B = 0.4$, $D_G = 0.4$. See Table 5.1 for parameter descriptions.

So far, we assumed that trees and grasses are competitors with equal characteristics. We further simulated trees and grasses as function of the competitive strength of grasses (α) and the resource use efficiency of trees (e_W) (Figure 5.5A). If the competitive strength of grasses is low, grasses will hardly reduce tree growth and trees will suppress grasses. If grasses are superior competitors, they will suppress trees almost completely. With increasing resource use efficiency of the trees, the ability of the trees to survive increases, despite the fact that grasses are better competitors. Figure 5.5B shows that higher local biomass densities can be reached compared to a homogeneous environment if patterns are formed (compare cross-section in Figure 5.2B). When grasses change from inferior competitor to superior competitor, a range of different patterns is produced from tree-dominated savannas to grass-dominated savannas. In the range of α where both trees and grasses co-occur, the positive effect of α on grasses is buffered by the response of grazers, resulting in an increasing grazer pressure and a seemingly stable peak standing biomass for grasses (Figure 5.5B).

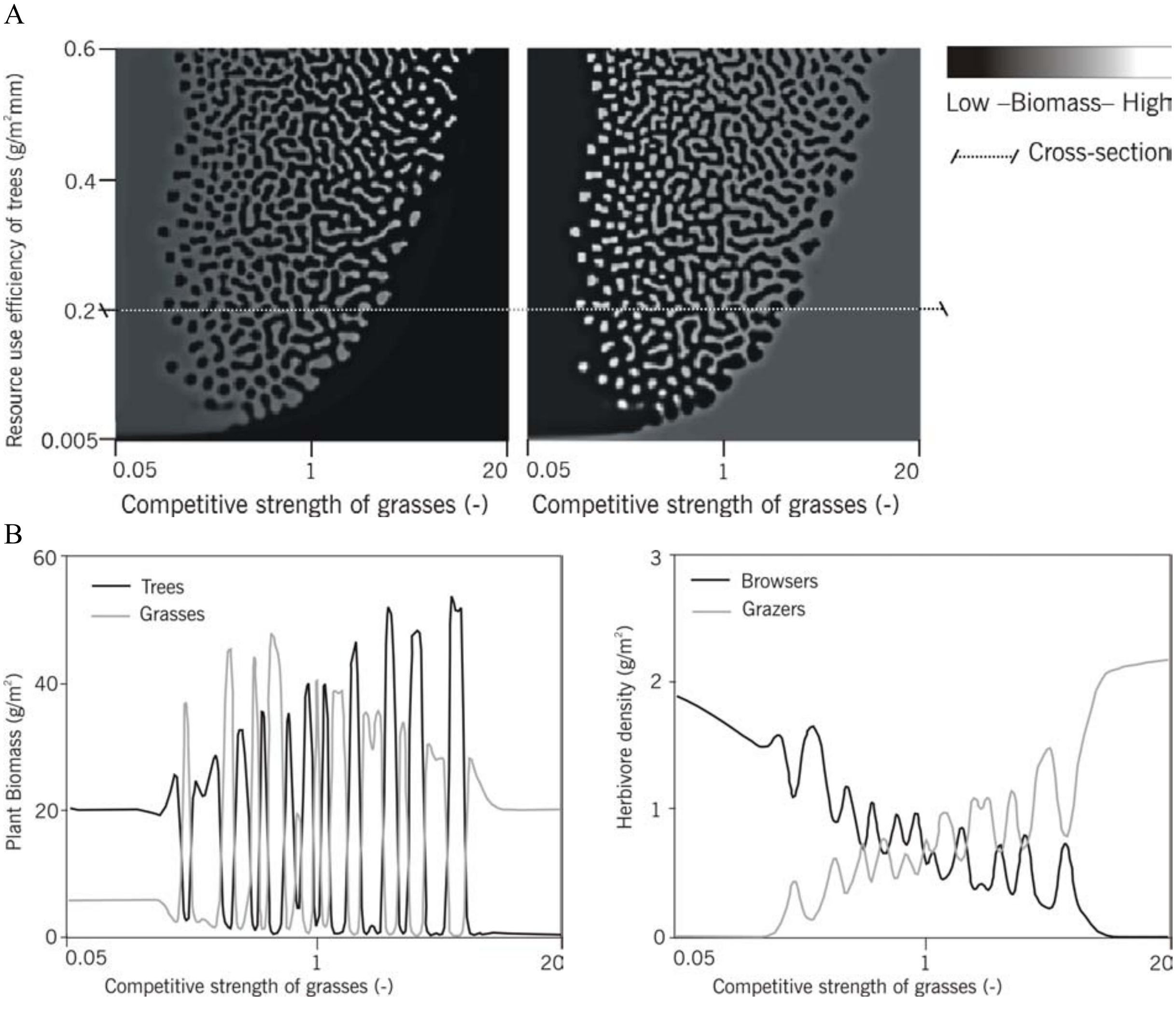


Figure 5.5 (A) Spatial patterns of trees (left) and grasses (right) for increasing competition strength of grasses (α) along the x-axis and resource use efficiency of trees (e_W) along the y-axis. (B) Cross-section over a gradient of the competitive strength of grasses for woody and grass biomass (left) and grazer and browser density (right) at $e_W = 0.2$. The simulations cover a spatial grid of 200×200 cells with size of 2.5×2.5m. Initial conditions are: $W = 20$, $H = 1$, $G = B = 0.4$. Other parameters are: $r = 12$, $\mu = 0.2$, $k_W = 10$, $k_H = 10$, $c_G = 0.01$, $c_B = 0.01$, $m_W = 0.002$, $m_H = 0.002$, $e_H = 0.2$, $g_B = 0.05$, $g_G = 0.05$, $m_B = 0.01$, $m_G = 0.01$, $\beta = 1$, $D_W = 0.005$, $D_H = 0.005$, $D_B = 0.4$, $D_G = 0.4$. See Table 5.1 for parameter descriptions.

Discussion

In this paper, we show that spatial patterns in savanna trees and grasses can be explained by resource competition between trees and grasses and herbivory. These patterns are self-organising because regular patterns in trees and grasses occur, regardless of initial conditions. We found that patterns in vegetation can emerge when consumers that are attracted to high plant biomass of the superior competitor facilitate the growth of the inferior competitor in the surroundings. In this explanation, the spatial scale of these processes is crucial as there is local competition between trees and grasses and large-scale facilitation of the one growth form by consumers of the other growth form. We illustrate this for trees and browsers. Trees are self-enhancing (*i.e.*, tree growth leads to further tree growth until a maximum) and browsers are attracted to locations with high woody biomass. Although browsers consume woody biomass at these locations, woody biomass will not be reduced here completely as browsing pressure is a function of woody biomass, and thus browsers leave these locations when woody biomass decreases. Furthermore, browsers do not only forage at the locations with high woody biomass but also in their surroundings. In these surroundings, woody biomass was already lower than at the locations to which the browsers were attracted, and browsing reduces woody biomass here. Consequently, grasses are able to increase in the surroundings of locations with high woody biomass, and further reduce tree growth. By doing so, browsing decreases the competitive effect of trees on grasses in the surroundings of high woody biomass, and they amplify the spatial heterogeneity in woody biomass. This mechanism also works for grasses and grazer pressure.

Our model provides therefore a more general explanation for patterns in savanna trees and grasses over a range of environmental conditions than the ones proposed before (see Archer 1989, 1990, Archer *et al.* 1988, Jeltsch *et al.* 1996, 1997, 1998, Olff *et al.* 1999, Van Wijk & Rodriguez-Iturbe 2002, Lejeune *et al.* 2002). We also found that patterns are possible when one of the growth forms is competitively superior, given that the specific herbivore reduces this competitively superior growth form in the surroundings of local biomass concentrations. Under some conditions (*e.g.*, low rainfall), grasses might be competitively superior, whereas trees dominate under other conditions (*e.g.*, high rainfall, Sankaran *et al.* 2005). Our model could be applied to both cases and only needs, apart from trees and grasses that compete for a limiting resource (*i.e.*, soil water or nutrients), consumers (grazers and browsers) to realise pattern formation, in contrast to models that need spatial heterogeneity in environmental conditions (Jeltsch *et al.* 1996, 1997, 1998) or temporal variability in climatic conditions (Van Wijk & Rodriguez-Iturbe 2002). Since browsers and/or grazers are present in many savannas worldwide, and trees and grasses often compete for a shared resource (Scholes & Archer 1997), our model is generally applicable.

We predict a gradient of pattern types between the homogenous cover of one of the two growth forms: from spots to labyrinth to gaps. We found patterns in savanna trees and grasses under very different levels of resource availability, which could be soil water or nutrients, and for different plant characteristics. The shape and scale of the simulated patterns resemble the patterns found in nature (Figure 5.1). The next step would be to systematically investigate how patterns in trees and grasses change over environmental gradients, such as rainfall. In general, we can conclude that spotted patterns of either trees or grasses are the result of a competitive disadvantage, either by a higher loss due to the accompanying herbivore or a lower competitive effect on the other competitor. The dominance of tree spots in savannas is caused by the lower regenerative ability of trees compared to grasses. Because trees do not regenerate as fast as grasses after a disturbance (such as fire), they have a competitive disadvantage and an increase in grass biomass can be expected. Some studies show a transition from grassland to tree dominance along a rainfall gradient (Archer 1989, 1990, Van Wijk & Rodriguez-Iturbe 2002, Sankaran *et al.* 2005). This transition is expected to be the result of grasses as superior competitor at low rainfall sites, and trees as better competitor at the other end of the continuum. We hypothesise that along this gradient, patterns of trees and grasses change from tree spots to grass spots in a landscape dominated by trees. We also predict a changing pattern as the dominant herbivore species changes, for example, from bigger to smaller browsers (Figure 5.4).

Our model corresponds with the key ingredient for patterns in a multi-species competitive system (Holmes *et al.* 1994, p. 25): "Multi-species competition systems will produce patterns if indirect interactions occur such that the increase of one species indirectly increases the growth of another...". Meinhardt (1995) also suggests support for the increase in the one competitor as result of the increase in the other as mechanism for pattern formation on seashells. In our model, the one growth form (either trees or grasses) indirectly stimulate the growth of the other form by large-scale consumption of the accompanying herbivores that are attracted to its high plant biomass.

Recent theory in ecology shows that such scale-dependent interaction between facilitation and competition can generate complex spatial structure in ecosystems (Lejeune *et al.* 1999, Rietkerk *et al.* 2004, Van de Koppel *et al.* 2005). Several studies present small-scale facilitation through soil shading and root enhancement of soil permeability and large-scale competition for resources as explanation for vegetation patterns in arid regions. Patterns can take the form of banding or regular patches (Klausmeier 1999, Couteron & Lejeune 2001, Rietkerk *et al.* 2002, 2004). Similar patterns in mussel beds can be modelled assuming facilitation at small scale and competition at larger scales (Van de Koppel *et al.* 2005, Gascoigne *et al.* 2005). In contrast to these studies, we found that patterns in vegetation can also emerge when competition operates at local scale whereas consumers facilitate growth of the inferior competitor at larger scale. With this finding, our study contributes to the growing body of evidence for common mechanisms for pattern formation in biological systems.

Acknowledgements

We are grateful to Hans Stigter, Hans Meinhardt, Stefan Dekker and Max Rietkerk for their useful comments and discussion.

APPENDIX 5.1.
Formal stability analysis of equilibria of the model consisting of equations 2-5

The model has three relevant equilibria, namely one internal equilibrium and two boundary equilibria. The internal equilibrium is defined as

$$\dot{W} = \frac{m_B}{c_B g_B} \quad \dot{H} = \frac{m_G}{c_G g_G} \tag{A1.1}$$

$$\dot{B} = -\frac{m_W}{c_B} + \frac{e_W g_B k_W r\mu}{m_B\left(k_W + \frac{m_G^2 \alpha}{c_G^2 g_G^2}\right)} \quad \dot{G} = -\frac{m_H}{c_G} + \frac{e_H g_G k_H r\mu}{m_G\left(k_G + \frac{m_B^2 \beta}{c_B^2 g_B^2}\right)}$$

Boundary equilibrium 1 is derived as

$$\dot{W}_{b1} = \frac{m_B}{c_B g_B} \quad \dot{H}_{b1} = \frac{e_H k_H r\mu}{m_H\left(k_H + \frac{m_B^2 \beta}{c_B^2 g_B^2}\right)} \tag{A1.2}$$

$$\dot{B}_{b1} = -\frac{m_W}{c_B} + \frac{e_W g_B k_W r\mu}{m_B\left(k_W + \frac{e_W^2 k_W^2 r^2 \alpha\mu^2}{m_H^2\left(k_H + \frac{m_B^2 \beta}{c_B^2 g_B^2}\right)^2}\right)} \quad \dot{G}_{b1} = 0$$

and boundary equilibrium 2 as

$$\dot{W}_{b2} = \frac{e_W k_W r\mu}{m_W\left(k_W + \frac{m_G^2 \alpha}{c_G^2 g_G^2}\right)} \qquad \dot{H}_{b2} = \frac{m_G}{c_G g_G} \tag{A1.3}$$

$$\dot{B}_{b2} = 0 \qquad \dot{G}_{b2} = -\frac{m_H}{c_G} + \frac{e_H g_G k_H r\mu}{m_G\left(k_H + \frac{e_W^2 k_W^2 r^2 \beta\mu^2}{m_W^2\left(k_W + \frac{m_G^2 \alpha}{c_G^2 g_G^2}\right)^2}\right)}$$

To investigate the local stability of these three equilibria, we investigated the Jacobian matrix of this model for each of these equilibria (Edelstein-Keshet 1988)

$$J = \begin{bmatrix} a_{11} & a_{12} & a_{13} & a_{14} \\ a_{21} & a_{22} & a_{23} & a_{24} \\ a_{31} & a_{32} & a_{33} & a_{34} \\ a_{41} & a_{42} & a_{43} & a_{44} \end{bmatrix} \tag{A1.4}$$

where the elements are determined as

$$a_{11} = \frac{\frac{\partial W}{\partial t}}{\partial W} \quad a_{12} = \frac{\frac{\partial W}{\partial t}}{\partial B} \quad a_{13} = \frac{\frac{\partial W}{\partial t}}{\partial H} \quad a_{14} = \frac{\frac{\partial W}{\partial t}}{\partial G} \tag{A1.5}$$

This is also done for a_{21}, a_{22}, a_{23}, a_{24}, a_{31}, a_{32}, a_{33}, a_{34}, a_{41}, a_{42}, a_{43} and a_{44}. To find the eigenvalues of the model, we set

$$\det(J-\lambda I)=0 \tag{A1.6}$$

This will lead to

$$0=\lambda^4+a_1\lambda^3+a_2\lambda^2+a_3\lambda+a_4 \tag{A1.7}$$

According to the Routh-Hurwitz criteria for four species (Edelstein-Keshet 1988), an equilibrium is stable when all the following conditions are satisfied

$$a_1>0 \tag{A1.8a}$$

$$a_3>0 \tag{A1.8b}$$

$$a_4>0 \tag{A1.8c}$$

$$a_1a_2a_3>a_3^2+a_1^2a_4 \tag{A1.8d}$$

APPENDIX 5.2.
Formal Turing analysis of equilibria of the model consisting of equations 2-5

To explore if the model leads to stable patterns a small spatially heterogeneous perturbation $\theta(x,y,t)$ in the homogeneous stable equilibrium $\dot{W}(x,y,t)$ is introduced. The coordinates *x* and *y* will be written as $\vec{x}$.

$$W(\vec{x},t) = \dot{W}_1 + \theta(\vec{x},t) \tag{A2.1a}$$

$$B(\vec{x},t) = \dot{B} + \beta(\vec{x},t) \tag{A2.1b}$$

$$H(\vec{x},t) = \dot{H} + \sigma(\vec{x},t) \tag{A2.1c}$$

$$G(\vec{x},t) = \dot{G} + \delta(\vec{x},t) \tag{A2.1d}$$

These are incorporated into the linearised system:

$$\frac{\partial\theta(\vec{x},t)}{\partial t} = a_{11}\theta(\vec{x},t) + a_{12}\beta(\vec{x},t) + a_{13}\sigma(\vec{x},t) + a_{14}\delta(\vec{x},t) + D_W\left(\frac{\partial^2\theta(x,t)}{\partial x^2} + \frac{\partial^2\theta(y,t)}{\partial y^2}\right) \tag{A2.2a}$$

$$\frac{\partial\beta(\vec{x},t)}{\partial t} = a_{21}\theta(\vec{x},t) + a_{22}\beta(\vec{x},t) + a_{23}\sigma(\vec{x},t) + a_{24}\delta(\vec{x},t) + D_B\left(\frac{\partial^2\beta(x,t)}{\partial x^2} + \frac{\partial^2\beta(y,t)}{\partial y^2}\right) \tag{A2.2b}$$

$$\frac{\partial\sigma(\vec{x},t)}{\partial t} = a_{31}\theta(\vec{x},t) + a_{32}\beta(\vec{x},t) + a_{33}\sigma(\vec{x},t) + a_{34}\delta(\vec{x},t) + D_H\left(\frac{\partial^2\sigma(x,t)}{\partial x^2} + \frac{\partial^2\sigma(y,t)}{\partial y^2}\right) \tag{A2.2c}$$

$$\frac{\partial\delta(\vec{x},t)}{\partial t} = a_{41}\theta(\vec{x},t) + a_{42}\beta(\vec{x},t) + a_{43}\sigma(\vec{x},t) + a_{44}\delta(\vec{x},t) + D_G\left(\frac{\partial^2\delta(x,t)}{\partial x^2} + \frac{\partial^2\delta(y,t)}{\partial y^2}\right) \tag{A2.2d}$$

To solve these four partial differential equations, it is necessary to rewrite the diffusion part of the equations. For this reason, $\theta(\vec{x},t)$ is replaced by $\dot{\theta}(t)\cos(q_1x)\times\cos(q_2y)$

$$\theta(\vec{x},t) = \dot{\theta}(t)\cos(q_1x)\times\cos(q_2y) \tag{A2.3a}$$

$$\beta(\vec{x},t) = \dot{\beta}(t)\cos(q_1x)\times\cos(q_2y) \tag{A2.3b}$$

$$\sigma(\vec{x},t) = \dot{\sigma}(t)\cos(q_1x)\times\cos(q_2y) \tag{A2.3c}$$

$$\delta(\vec{x},t) = \dot{\delta}(t)\cos(q_1x)\times\cos(q_2y) \tag{A2.3d}$$

Fill in equation (A2.3a) in equation (A2.2a) and cancel $\cos(q_1x)\times\cos(q_2y)$ leads to

$$\frac{\partial\dot{\theta}(t)}{\partial t} = a_{11}\dot{\theta}(t) + a_{12}\beta(t) + a_{13}\sigma(t) - D_W\left(\dot{\theta}(t)(q_1^2+q_2^2)\right)$$

Doing the same for β, σ and δ and replace $(q_1^2+q_2^2)$ by Q^2

$$\frac{\partial\dot{\theta}(t)}{\partial t} = a_{11}\dot{\theta}(t) + a_{12}\dot{\beta}(t) + a_{13}\dot{\sigma}(t) + a_{14}\dot{\delta}(t) - D_W\left(\dot{\theta}(t)Q^2\right) \tag{A2.4a}$$

$$\frac{\partial\dot{\beta}(t)}{\partial t} = a_{21}\dot{\theta}(t) + a_{22}\dot{\beta}(t) + a_{23}\dot{\sigma}(t) + a_{24}\dot{\delta}(t) - D_B\left(\dot{\beta}(t)Q^2\right) \tag{A2.4b}$$

$$\frac{\partial\dot{\sigma}(t)}{\partial t} = a_{31}\dot{\theta}(t) + a_{32}\dot{\beta}(t) + a_{33}\dot{\sigma}(t) + a_{34}\dot{\delta}(t) - D_H\left(\dot{\sigma}(t)Q^2\right) \tag{A2.4c}$$

$$\frac{\partial \dot{\delta}(t)}{\partial t} = a_{41}\dot{\theta}(t) + a_{42}\dot{\beta}(t) + a_{43}\dot{\sigma}(t) + a_{44}\dot{\delta}(t) - D_G\left(\dot{\delta}(t)Q^2\right) \qquad \text{(A2.4d)}$$

To investigate stability of the internal equilibrium point after perturbation a new Jacobian matrix is used

$$J_b = \begin{bmatrix} b_{11} & b_{12} & b_{13} & b_{14} \\ b_{21} & b_{22} & b_{23} & b_{24} \\ b_{31} & b_{32} & b_{33} & b_{34} \\ b_{41} & b_{42} & b_{43} & b_{44} \end{bmatrix}$$

with the elements:

$$\begin{array}{llll} b_{11} = a_{11} - D_W Q^2 & b_{12} = a_{12} & b_{13} = a_{13} & b_{14} = a_{14} \\ b_{21} = a_{21} & b_{22} = a_{22} - D_B Q^2 & b_{23} = a_{23} & b_{24} = a_{24} \\ b_{31} = a_{31} & b_{32} = a_{32} & b_{33} = a_{33} - D_H Q^2 & b_{34} = a_{34} \\ b_{41} = a_{41} & b_{42} = a_{42} & b_{43} = a_{43} & b_{44} = a_{44} - D_G Q^2 \end{array}$$

Now the stability of the equilibria can be investigated using the Routh-Hurwitz criteria for four species (equations A1.8a-d in Appendix 5.1). For pattern formation, the equilibria of the non-spatial model need to be stable (see Appendix 5.1), but the equilibria of the spatial model (equations A2.4a-d) need to be unstable.

CHAPTER 6

Dynamic interactions between vegetation and herbivore populations increase the stability of savannas

THOMAS A. GROEN, CLAUDIUS A.D.M. VAN DE VIJVER, HERBERT H.T. PRINS & FRANK VAN LANGEVELDE

Abstract

In this paper we investigate the effect that dynamic interactions between vegetation and herbivore populations have on the occurrence of alternative stable states in savannas, and the consequences for stability. Savannas can have alternative stable states when a positive feedback mechanism between fuel load (grass biomass), fire intensity and damage to trees exists. Then a state where both trees and grasses co-occur exist (savanna) and a state where only trees occur exists (*i.e.*, woodland). Grazing has a direct effect on this positive feedback because through removal of grass biomass the positive feedback can be reversed. Browsing on the other hand can induce this positive feedback. The effects of grazing and browsing on this positive feedback have been investigated, but only by assuming constant herbivore densities. By including an interaction between herbivore population growth and forage availability a negative feedback is introduced, that modifies the positive fire feedback in the system. We compared the model with constant herbivore densities, with the model with dynamically responding herbivore populations. We find that when herbivores respond dynamically to forage availability, the occurrence of alternative stable states is reduced compared to the model with constant herbivore densities. Alternative stable states can occur only when herbivores respond slowly to increments in forage availability —*i.e.*, low growth rates—, and have high mortality rates. These conditions allow for the occurrence of both savanna and woodland as stable states, where otherwise only woodland would be the stable state. Also, savanna occurs as a stable state over a wider range of environmental parameters when herbivores respond dynamically to forage availability. In other words, savannas as a stable state are promoted when herbivores respond dynamically to forage availability, as compared to situations where herbivore densities are kept constant.

Keywords: *herbivory; fire; grazing; browsing; alternative stable states; savanna; modelling; positive feedbacks; negative feedbacks.*

Introduction

Savannas cover an eight of the world's land surface (Scholes & Archer 1997) and harbour around one fifth of the world's population (Hoffmann *et al.* 2002). Savannas are characterized by a continuous grass layer and a discontinuous layer of trees and shrubs (Scholes & Archer 1997), which is variable in cover (Sankaran *et al.* 2005). The tree to grass ratio is determined by several factors, including rainfall, soil type, herbivore pressure and fire occurrence and intensity (Bond *et al.* 2005, Van Langevelde *et al.* 2003). Savanna ecosystem dynamics are of particular interest in ecology, because savannas are spatially heterogeneous ecosystems and can show sudden shifts between a low biomass system state (*i.e.*, tree-grass co-dominance) and a high biomass system state (*i.e.*, tree dominance; Briggs *et al.* 2002, Brown & Carter 1998, Roques *et al.* 2001, Van Auken 2000).

Due to the spatial heterogeneity, the importance of spatial processes like herbivory and fire, and because two competing life forms co-occur under many environmental conditions, savannas provide an ideal ecosystem to investigate several ecologically important processes such as competition and facilitation.

Additionally, the abundance of grass biomass versus tree biomass has important implications for the productivity of extensive farming systems based on cattle ranging (Janssen *et al.* 2004).

In the past decade the rapid transition of savannas containing both trees and grasses into ecosystems dominated by trees (so called bush encroachment) has become a serious point of concern (Brown & Carter 1998, Van Auken 2000). It has been suggested that the sudden shift from tree-grass co-existence towards tree dominance can be the result of the positive feedback mechanism between fuel load (grass biomass) and fire intensity, which could lead the system towards either a savanna state with trees and grasses or a tree-dominated state (Bond & Keeley 2005, Van Langevelde *et al.* 2003). The occurrences of these "alternative stable states" have been analysed in detail for several ecosystems including shallow freshwater lakes (Carpenter *et al.* 1999, Scheffer *et al.* 1997), coral reefs (Knowlton 1992, Nystrom *et al.* 2000) and arid grasslands (Rietkerk & Van de Koppel 1997). An important feature of ecosystems having alternative stable states is the prediction that they are vulnerable for abrupt discontinuous changes, so called "catastrophic shifts". This has been observed in several ecosystems (Rietkerk & Van de Koppel 1997, Scheffer *et al.* 2001, Scheffer & Carpenter 2003).

Burning is a common phenomenon in savanna ecosystems (Bond *et al.* 2005, Carmona-Moreno *et al.* 2005, Trollope *et al.* 2004) and can have profound effects on the tree-grass balance in savannas, depending on a variety of factors as climatic conditions, tree height and fuel load (Govender *et al.* 2006, Trollope *et al.* 2004, West 1965). The damaging effect of fire on trees increases with fire intensity (De Ronde *et al.* 2004) which is determined by a number of factors, including grass biomass with more grass biomass resulting in more intense fires. As mentioned before, herbivory is another determinant of savanna structure and dynamics. The effects of herbivory can be direct for example through tree removal (Dublin *et al.* 1990) or suppression of seedling establishment (Loth *et al.* 2005, Prins & Van der Jeugd 1993). But herbivory effects can also be indirect, via removal of grass biomass which accordingly can reduce fire intensity and thus the effect of fire on trees. This can initiate the before mentioned positive feedback where reduced fire intensity leads to less damage to trees and thus higher tree cover which consequently reduces grass cover. Previous modelling studies predicted the occurrence of alternative stable states on the basis of the interaction of between herbivores and disturbances like fire (D'Odorico *et al.* 2006, Dublin *et al.* 1990, Van Langevelde *et al.* 2003). An important assumption in these models was that grazing and browsing pressure is constant. In human-managed systems this assumption might hold, but in natural systems certainly not. The population dynamics and distribution of wild herbivore populations are largely determined by available resources (Owen-Smith & Mills 2006). Previous studies on the effect of dynamic herbivore populations on the stability of arid grasslands showed that with dynamic herbivore populations, the stability of the system increases and the chances of catastrophic shifts are reduced considerably (Van de Koppel & Rietkerk 2000). When considering grazing and browsing in savannas, however, the direct and in direct effects of grazers on browsers and vice versa, and their interactive effects on the positive feedback mechanism are so far unexplored. Using a model, we investigate the effect that these dynamic herbivore populations might have on savanna ecosystem stability where the positive feedback mechanism between fuel load and fire intensity is active.

The model

Plants

We modelled savanna ecosystems using the equations in Van Langevelde *et al.* (2003). The model simulates changes in grass and woody biomass. Grass biomass comprises both grasses and herbaceous plants, while woody biomass comprises wood, twigs and leaves. We assume that trees and grasses compete for water, that trees have access to both top (w_t) and that sub (w_s) soil layers and that grasses only have access to the top soil layer (Knoop & Walker 1985, Schenk & Jackson 2002, Walker & Noy-Meir 1982). We also assume that grasses are better competitors for water in the top soil layer (Jackson *et al.* 1996). This makes the modelling of tree-grass competition essentially the same as the model previously described by Walker *et al.* (1981) and Walker and Noy-Meir (1982). The model simulates with time steps of 1 year. All parameters with their description and units are listed in Table 6.1.

The rate of moisture recharge into the top soil layer is the amount of infiltrated water (w_{in}) minus the loss of water to the subsoil layer (w_s):

$$w_t = w_{in} - w_s \tag{1}$$

The amount of water that infiltrates to the sub soil layer is proportional to the amount of water that infiltrates in the top soil:

$$\begin{aligned} w_s &= \alpha(w_{in} - \beta) \qquad && w_{in} > \beta \\ w_s &= 0 && w_{in} \le \beta \end{aligned} \tag{2}$$

where β is the amount of water in the top soil layer above which water starts to percolate to the sub soil layer and α is the proportion of water that starts to percolate.

The proportion of water uptake from the upper soil layer per unit grass biomass is defined as (Walker *et al.* 1981)

$$U_H = \frac{\theta_H}{H\theta_H + W\theta_W + w_s} \tag{3}$$

where θ_H and θ_W are the water uptake rates of grasses and trees respectively, H and W are the amount of grass and woody biomass respectively, and w_s is the amount of water lost through percolation to the sub soil. Water is used by plants for production of new biomass, and the utilization of water by grasses for production of new grass biomass is expressed by the fraction of the total amount of water in the top soil taken

up by grasses ($U_H H$) times the amount of water in the top soil (w_t) times the water use efficiency of the grasses (r_H). Total change in the amount of grass biomass in the model is expressed as

$$\frac{dH}{dt} = r_H w_t H \frac{\theta_H}{H\theta_H + W\theta_W + w_s} - d_H H - c_H GH - k_H nH \qquad (4)$$

including mortality due to senescence ($d_H H$), grazing ($c_H GH$) and loss due to fire ($k_H nH$).

Table 6.1 Overview of the variables and parameters used in the model. Parameter values are taken from Van Langevelde *et al.* (2003), and references therein.

Symbols	Interpretation	Units	Values
H	Grass biomass	g m^{-2}	0-400
W	Woody biomass	g m^{-2}	0-1000
r_H	Water use efficiency of grasses	g mm^{-1}	1.0
r_W	Water use efficiency of trees	g mm^{-1}	0.5
θ_H	Rate of water uptake per unit grass biomass	mm yr^{-1} g^{-1}	0.9
θ_W	Rate of water uptake per unit woody biomass	mm yr^{-1} g^{-1}	0.5
d_H	Specific loss of grass biomass due to senescence	yr^{-1}	0.9
d_W	Specific loss of woody biomass due to senescence	yr^{-1}	0.4
d_G	Specific mortality rate of grazers	m^2 g^{-1} yr^{-1}	0.02
d_B	Specific mortality rate of browsers	m^2 g^{-1} yr^{-1}	0.02
c_H	Consumption coefficient of grass biomass by grazers	m^2 g^{-1} yr^{-1}	0.02
c_W	Consumption coefficient of woody biomass by browsers	m^2 g^{-1} yr^{-1}	0.02
e_H	Coefficient for consumption and conversion efficiency of grass biomass by grazers	m^2 g^{-1} yr^{-1}	0-0.001
e_W	Coefficient for consumption and conversion efficiency of woody biomass by browsers	m^2 g^{-1} yr^{-1}	0-0.001
k_H	Specific loss of grass biomass due to fire	yr^{-1}	0.1
k_W	Specific loss of woody biomass due to fire expressed per unit of energy	W^{-1}	0.01
n	Frequency of fire per year	yr^{-1}	0 or 1
a	Coefficient for the increase in fire intensity with grass biomass	W m^{-1} g^{-1}	0.5
α	Proportion of excess water that percolates to sub soil layer	-	0.4
β	Soil moisture content in the top soil layer above which water starts to percolate to the sub soil layer	mm	200-500
w_{in}	Annual amount of infiltrated water	mm m^{-2} yr^{-1}	0-1000
w_t	Available amount of water in the top soil layer	mm m^{-2} yr^{-1}	see eqn. 1
w_s	Available amount of water in the sub soil layer	mm m^{-2} yr^{-1}	see eqn. 2
G	Grazer density	g m^{-2}	0-30
B	Browser density	g m^{-2}	0-15

For woody biomass, the equation is similar except for the uptake of water, because trees also have access to the sub soil layer, and for the effect of fire on trees where grass biomass determines the severity of burning. Water uptake from the top soil layer by trees is formulated in a similar fashion to that for grasses:

$$U_W = \frac{\theta_W}{H\theta_H + W\theta_W + w_s} \tag{5}$$

Because trees also have access to water in the sub soil layer, the total rate of change in woody biomass is:

$$\frac{dW}{dt} = r_W\left[w_t W \frac{\theta_W}{H\theta_H + W\theta_W + w_s} + w_s\right] - d_W W - c_W BW - k_W anHW \tag{6}$$

where the last term ($k_W anHW$) expresses the loss of tree biomass due to fire which is a function of fire frequency (n), the specific loss of biomass due to fire per unit heat released (k_W), the amount of grass biomass present (H) and the heat yield per g of grass biomass (a).

The effect of fire on trees is mostly limited to small trees, whereas large trees hardly suffer any damage of fires (De Ronde *et al.* 2004). Also the effect of browsing on trees might not be the same as trees grow out of reach for most browsers (Chapter 5, Cameron & Du Toit 2007), and small trees are likely to suffer more from browsing than large trees but it has been shown that mature trees also suffer from browsing (Goheen *et al.* 2007). We therefore modelled trees occurring in the most susceptible range to fire and herbivory, being up to 5 meters (De Ronde *et al.* 2004).

Herbivores

The consumption of plant biomass by the grazer (G) and browser (B) populations was modelled assuming a linear numerical response. Increments in herbivore biomass occur as a result of the intake rate of plant biomass and the conversion efficiency of consumed plant biomass into herbivore biomass. We combined these properties into one parameter for grazers (e_H) and one for browsers (e_W), assuming that both are constants (Prins 1993). We assume a density dependent growth function (Fowler 1987, Hanski 1990) resulting in the following equations describing herbivore dynamics:

$$\frac{dG}{dt} = e_H GH - d_G G^2 \tag{7}$$

$$\frac{dB}{dt} = e_W BW - d_B B^2 \tag{8}$$

Analysis

We analysed the stability of the equilibria of the model with extensive simulations. We simulated the model with parameter values as presented in Van Langevelde *et al.* (2003) and references within. For each combination of parameters we simulated with different initial densities of grass biomass to make sure that if alternative stable states exist the simulations started in the different domains of attraction. We varied water availability (w_{in}), the efficiency with which the grazers consume and convert grass biomass (e_H), the specific mortality rate of grazers (d_G) and fire frequency (n) over realistic ranges of values to analyse the behaviour of the model. Parameters e_H and d_G determine the speed of the response of the herbivore population to changes in forage availability. With high values of e_H, the grazer population grows fast with an increment in grass biomass. With high d_G, the grazer populations' mortality rate is high, making that the consumption of grass has to be high in order to maintain the population density, and with a decrease of grass biomass, a rapid decline in grazer density is to be expected. We simulated the model with (1) constant grazer and browser populations (equations 4 and 6), (2) a dynamic grazer population and constant browser population (equations 4, 6 and 7), (3) a constant grazer population and dynamic browser population (equations 4, 6 and 8), and 4) dynamic grazer and browser populations (equations 4, 6, 7 and 8). When alternative stable states were found, the location of the separatrix was determined using simulations by initialising the model over a range of initial values of grass biomass. The separatrix indicates at which level of grass biomass in the ecosystem it switches from one stable state to an other stable state, given certain environmental conditions.

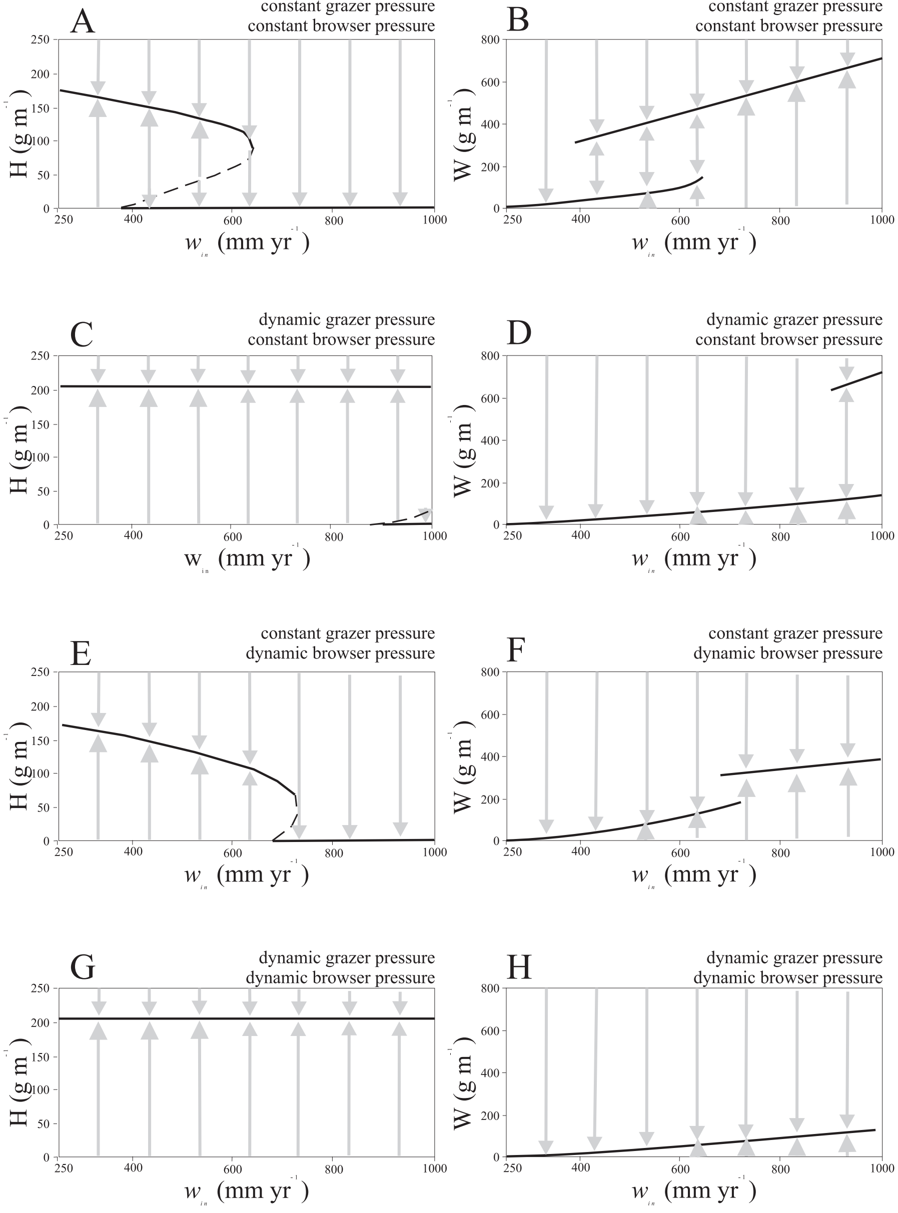


Figure 6.1 Stable equilibria (solid lines) for grasses (*H*) and trees (*W*) over a precipitation range (250-1000 mm) with different situations of herbivore dynamics: (A and B) constant grazer and browser pressure; (C and D) constant browsers pressure and dynamic grazer pressure; (E and F) constant grazer pressure and dynamic browser pressure and (G and H) dynamic grazer and browser pressure. The separatrix (dashed line) is obtained by running simulations with different initial values for *H*. Which equilibrium for *W* is selected depends on the initial value in *H*, and therefore this separatrix can not be shown. Grey arrows show to which equilibrium the system will develop, given a certain initial grass biomass. Parameters: $\alpha = 0.4$; $a = 0.5$; $c_H = c_W = 0.02$; $d_G = 0.02$; $d_B = 0.02$; $d_H = 0.9$; $d_W = 0.4$; $e_H = e_W = 0.001$; $k_H = 0.1$; $k_W = 0.01$; $n = 1$; $r_H = 1$; $r_W = 0.5$; θ_W=0.5; θ_H=0.9; β=250; *G*=15 (in A, B,E and F); *B*=5 (in A-D).

Results

In Figure 6.1, the effect of water availability (w_{in}) on grass and woody biomass for all analyses is presented, *i.e.*, no herbivore population dynamics (A,B), only grazer population dynamics (C,D), only browser population dynamics E,F) and both grazer and browser population dynamics (G,H). When herbivore populations are not modelled dynamically, increasing the water availability (w_{in}) drives the system from a

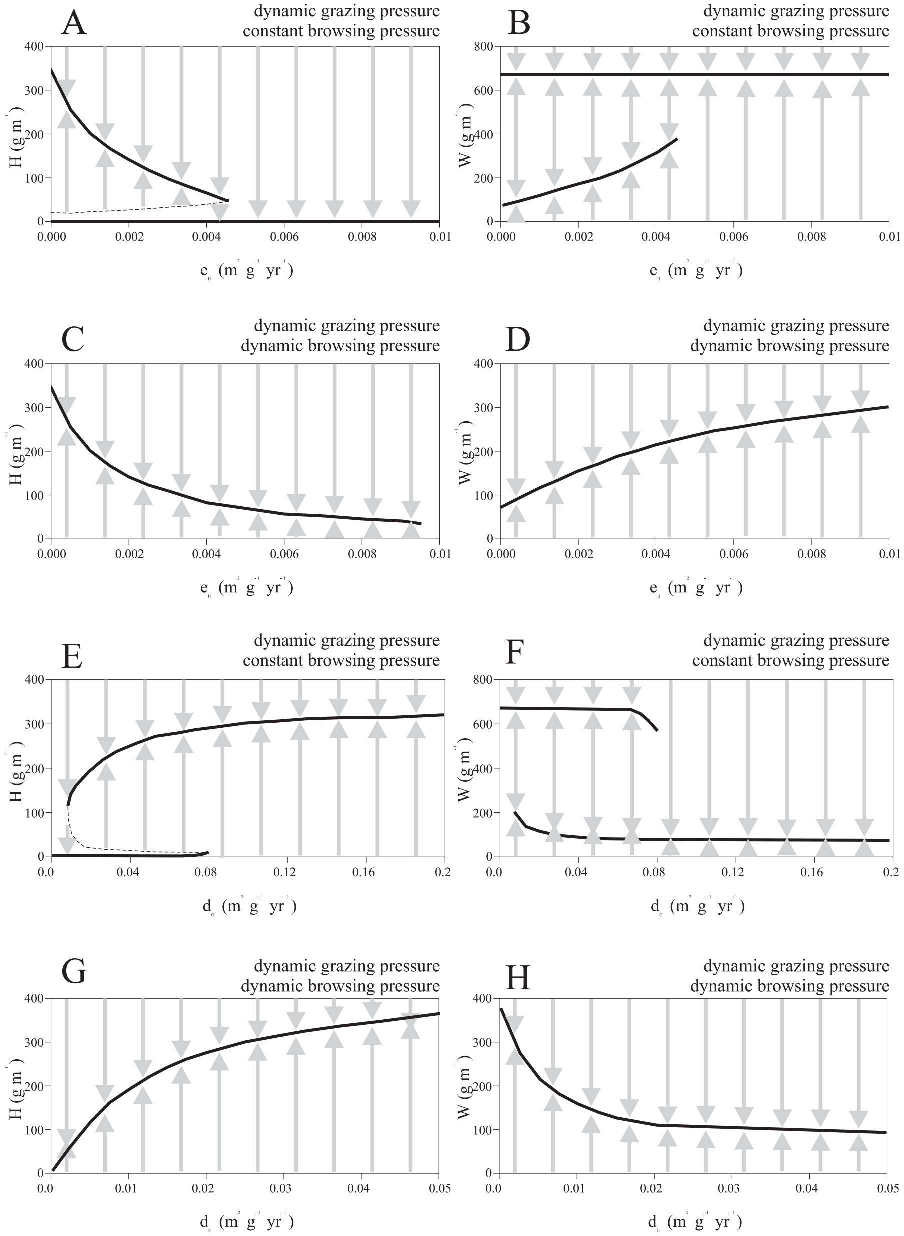


Figure 6.2 Stable equilibria (solid lines) for grasses and trees with dynamic grazers and static browsers (A, B, E and F) and dynamic grazers and browsers (C, D, G and H) at varying values for the conversion coefficient of grass biomass to grazer biomass (e_H in A-D) and the specific grazer mortality rate (d_G in E-H). The separatrix (dashed line) is obtained by running simulations with different initial values for *H*. Parameters: $\alpha = 0.4$; $a = 0.5$; $c_H = c_W = 0.02$; $d_G = 0.02$ (in A-D); $d_B = 0.02$; $d_H = 0.9$; $d_W = 0.4$; $e_W = 0.001$; $e_H = 0.001$ (in C – D); $k_H = 0.1$; $k_W = 0.01$; $n = 1$; $r_H = 1$; $r_W = 0.5$; θ_W=0.5; θ_H=0.9; β=250, w_{in}=940; *B*=5 (in A, B, E and F).

grassland system (data not shown, see Van Langevelde *et al*. 2003) via tree-grass co-occurrence (savanna) towards a woodland system (Figure 6.1 A, B). In regions of w_{in} with alternative stable states, both savanna and woodland can occur. These alternative stable states occur in most analyses (Figure 6.1 A-F) except when both the grazer and browser population is dynamic (Figure 6.1G and H). We simulated the latter even up to w_{in} = 2500 mm (data not shown), but this did not provide us with alternative stable states. In the model with constant grazer and browser numbers, alternative stable states occur at intermediate levels of w_{in}, while they occur at higher w_{in} levels when either the grazer or browser populations are simulated dynamically, and also the range of w_{in} where they occur decreases. Finally, savannas occur over a broader range of w_{in} when herbivore populations are dynamic.

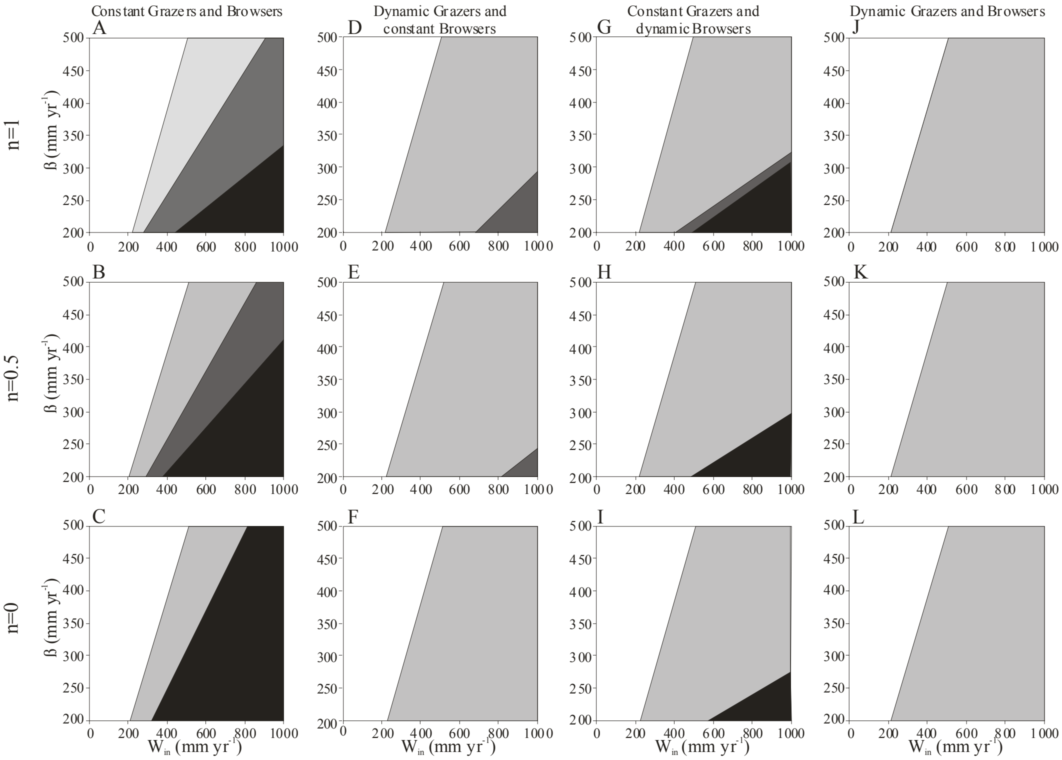


Figure 6.3 Parameter plane showing the output for different settings of annual water infiltration (w_{in}), percolation threshold above which water starts to percolate to the sub soil (β), and fire frequency (n). Other parameters: $\alpha = 0.4$; $a = 0.5$; $c_H = c_W = 0.02$; $d_G = 0.02$; $d_B = 0.02$; $d_H = 0.9$; $d_W = 0.4$; $e_H = e_W = 0.001$; $k_H = 0.1$; $k_W = 0.01$; $r_H = 1$; $r_W = 0.5$; $\theta_W = 0.5$; $\theta_H = 0.9$; $B = 5$ (in A-F); $G = 22$ (in A-C and G-I). □ = grassland; ▒ = savanna; ▓ = alternative stable states; ■ = woodland.

The effect of varying the efficiency with which the grazer population consumes and converts grass biomass (e_H) and the specific mortality rate of the grazer population (d_G) on grass and woody biomass are shown in Figure 6.2. When grazers are modelled dynamically but browser numbers are kept constant, alternative stable states exist only at low values of e_H (Figure 6.2 A and B). At higher values of e_H, the system switches to woodland without grass biomass. When browsers are modelled dynamically as well, savanna is the only stable equilibrium (Figure 6.2 C and D). Changing d_G leads to alternative stable states at intermediate values, while woodland occur at low values of d_G and savanna at high values (Figure 6.2 E and F). Again when we include browser dynamics as well, the alternative stable states disappear and only savanna occurs. Here, the abundance of grass biomass increases with increasing d_G (Figure 6.2 G and H).

To analyse the combined effect of water availability (w_{in}), soil water percolation threshold (β) and fire frequency (n), we simulated the model for a range of environmental conditions (Figure 6.3). Figure 6.3 A, B and C show that alternative stables states only occur in the presence of fire at the expense of woodland, and that the range increases when burning frequency increases (Van Langevelde *et al.* 2003). When including dynamic grazer or browser populations (Figure 6.3 D-I), the parameter range where alternative stable states occur decreases. When including both dynamic grazer and browser populations (Figure 6.3 J-L), alternative stable states and also woodland do not occur anymore within the ranges investigated. This concurs with the results in Figure 6.1. Figure 6.3 also shows the interaction between w_{in} and β. The positive effect of water availability (w_{in}) on tree dominance becomes less when β increases, because water is retained better in the top soil layer.

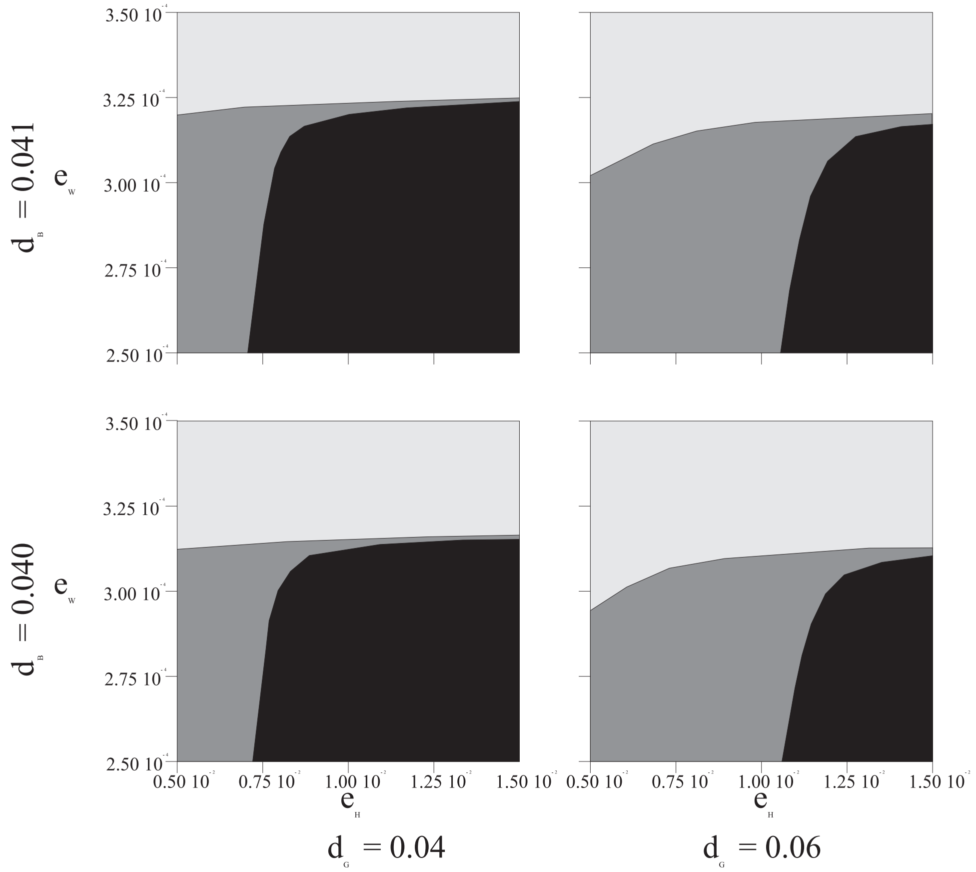


Figure 6.4 Parameter plane showing the output for different settings of eH and eW, and different levels of mortality (dG and dB) when both grazer and browser populations respond dynamically. Other parameters α = 0.4; a = 0.5; $c_H = c_W$ = 0.02; d_H = 0.9 ; d_W = 0.4; k_H = 0.1; k_W = 0.01; n = 1; θ_W = 0.5; θ_H = 0.9; r_H = 1; r_W = 0.5; w_{in} = 940; β = 250; d_G and d_B as indicated in the figure. Shades indicate same states as in Figure 6.3.

Figure 6.4 shows the effect of changing grazer and browser response to biomass availability (e_H and e_W), when both grazers and browsers are modelled dynamically. At very low values of e_H and e_W alternative stable states can occur, but when either one of the two parameters increases, *i.e.*, the population responds faster to increases in biomass, alternative stable states disappear, and either woodland or grassland is the resultant landscape. With increasing e_H, the grassland state is suppressed, and the resultant landscape is woodland. With increasing e_W, the woodland state is suppressed and the resultant landscape is savanna. When the mortality of grazers increases (c.f. Figure 6.4C with 4D), the parameter space of e_H and e_W where woodland can occur decreases, because grazers are less capable of suppressing the woodland state. Also, when the mortality of browsers increases, the parameter space where savannas can occur decreases because the browsers are less capable of suppressing the savanna state. The borders between the different states display convex monotonously increasing curves, suggesting that the sensitivity of the system to changes in e_H is high at low values, but decreases once this values increase. Also, the system is much more sensitive to changes in e_W than to changes in e_G (compare scales) and to changes in d_G and in d_B (compare different values).

Discussion

We analysed the effect of dynamically modelled herbivore populations and their direct and indirect interactions on the stability of savanna ecosystems. We show that including dynamic herbivore populations reduces the occurrence of alternative stable states and increases the occurrence of savanna compared with constant herbivore numbers (Figure 6.2). An decrease in parameter ranges where alternative stable states occur result in more stable savannas as these are the only conditions where sudden shifts from savanna to woodland (*i.e.*, bush encroachment) are expected. First, these results suggest that when herbivores respond dynamically to changes in food abundance, the occurrence of savannas is much more likely than under constant herbivore numbers. Second, they suggest that the risk of bush encroachment is reduced when herbivores respond dynamically because the range of conditions under which alternative stable states occur decrease. Third, dynamic herbivore populations increase the range of the savanna state considerably. Finally, when both grazer and browser populations are dynamic, the interaction between grazers and browsers becomes important in determining the equilibrium. Grazers suppress grass growth, and with that the competitive effect of grasses on trees. Trees are therefore performing better, which has an effect on the browser population. This facilitative effect of grazers on browsers and vice versa can exclude the occurrence of alternative stable states within the parameter ranges we investigated.

As is explained by Van Langevelde *et al.* (2003), the positive feedback between fuel load (grass biomass) and fire intensity results under certain conditions in alternative stable states. High amounts of grass biomass result in intense fires, which lead to severe damage to trees. The effect of grazers on this positive feedback mechanism diminishes when the grazer population responds dynamically to the available amount of grass biomass. A decrease in grass biomass due to consumption triggers a negative feedback as this reduced grass biomass also leads to a decrease in grazer density. This allows the grass to recover from herbivory and to provide fuel load for intense fires. This ensures a more stable presence of grass biomass in the system and the occurrence of savannas where otherwise woodland would occur.

An important factor that determines the effect of this negative feedback is the speed at which herbivores respond to changes in grass biomass. We investigated the effect of the speed of the herbivores response on the stability of savannas by varying the efficiency with which the grazers consume and convert grass biomass (e_H) and the specific mortality rate of the grazers (d_G). First, we found that the stability of savannas decreases with an increase in the response of grazer biomass to grass biomass (*i.e.*, high e_H). Second, the stability of savanna ecosystems increases with an increase in the specific mortality rate, *i.e.*, a rapid response of density-dependent mortality to increasing grazer biomass (*i.e.*, high d_G).

The speed at which grazer populations respond to forage presence is not necessarily only a function of mortality or consumption and conversion efficiency. At a larger scale, grazers migrate to locations with more food when forage becomes scarce reducing the effect of the grazers on the vegetation (Drent & Prins 1987, McNaughton 1979, Van de Koppel *et al.* 2002). We would expect that such migratory behaviour reduces the risk that savannas collapse into a bush-encroached state. Moreover, grazer populations, both wildlife (Owen-Smith & Ogutu 2003) and livestock (Toulmin,1994), follow climatic variability (Illius & O'Connor 1999). Our results suggest that when pastoralists respond quickly to decrease in forage availability and slowly to vegetation regeneration, the stability of the savannas increases and the risk on vegetation collapse decreases. However, it should be kept in mind that the response of herbivore populations depend on more than forage availability alone, like water accessibility, vegetation structure and predation risk. This means that savanna areas near water points can experience a higher grazing pressure than predicted by our model. Alternatively, areas with high predation risk or high tsetse densities can experience less grazing than predicted by our model, resulting in more stable savannas.

Our findings concur with findings by Van de Koppel and Rietkerk (2000) who found similar results for arid grasslands that can collapse and lose their vegetation under conditions of water stress and overgrazing. They modelled arid grasslands for abiotic conditions under which a shift from a vegetated state to bare soil is likely to occur, namely low water availability. Their system became more resilient to drought when they included grazer population dynamics. In our study, we consider mesic savannas, where, in the absence of disturbances, shifts to tree-dominated states are expected to occur (Sankaran *et al.* 2005, Van Langevelde *et al.* 2003), *i.e.*, we expect a shift from a low biomass state (grass dominance) towards a high biomass state (tree dominance). In this system, we have an interaction between grazers and browsers.

The interaction between grazers and browsers suggests that not only the speed of the response of grazers, but also suggests that the speed of the response of browsers is important for the dynamics of savanna ecosystems. Woody biomass decreases due to browsing, and modelling the browser population dynamically reduces the impact of browsers at low woody biomass densities and increases the impact at high woody biomass densities. The results show similar trends as for grazers, namely that the occurrence of alternative stable states disappears when the browser population responds to food availability. This suggests for savanna management that the use of browsers along with grazers (*e.g.*, a mixture of cows and goats) reduces the chances of bush encroachment.

Recently, it has been stated that the occurrence of bush encroachment is also affected by climatic change (Beerling & Osborne 2006, Bond *et al.* 2005). The increase in current CO_2 levels as well as the related rise in temperatures are indicated as important drivers that create favourable conditions for tree establishment and survival. Beerling and Osborne (2006) argue that whether these driving forces are effectively going to change the savanna biome depends strongly on whether management of these systems will focus on the woody or the grass component. Our results suggests that when more areas become prone to bush encroachment due to climatic chance, this effect can be at least partly mediated by changing the management of the system to more dynamically responding herbivore densities.

The focus from a management point of view in savanna dynamics often lies at the pastoralist and extensive cattle farm type of implications. From this point of view, maintaining a stable grass community is of importance to maintain cattle production. We showed that with focussing on the utilisation of both the grass and woody component of the system (*i.e.*, tracking climatic variability), the stability of the savanna biome can be increased, and its persistence under changing conditions perhaps ensured.

Our results provide insight in the interactive effects of both grazing and browsing on the dynamics in savanna ecosystems. An important conclusion is that the speed with which herbivore populations respond to changes in forage availability has consequences for the occurrence of alternative stable states, and therefore for sudden shifts in these systems.

Acknowledgements

We would like to express our gratitude to G.M. Hengeveld for his suggestions while working on this manuscript.

CHAPTER 7
The spatial scale of fire influences the stability of savanna ecosystems

THOMAS A. GROEN, FRANK VAN LANGEVELDE & CLAUDIUS A.D.M. VAN DE VIJVER

Abstract

This paper describes a spatially explicit model study investigating the effects of spatial processes and their scale on the stability of ecosystems. We modelled savannas that can shift between two alternative stable states: tree-grass co-occurrence and woody cover dominance. Fire is here a spatially explicit process as the size of the burned area is variable. Model results show that the range of environmental conditions (rainfall and soil properties) where these alternative stable states occur increases when fire is simulated spatially explicitly compared with simulations where fire occurs everywhere. Also, when the scale of burning increases, the range of environmental conditions where alternative stable states occur increases, and the system becomes more vulnerable for sudden shifts. Small-scale fire has a positive effect on the stability of savannas, while large-scale fire has a negative effect. In contrast to the results from the non-spatial model, the response of the ecosystem to increasing stress (*e.g.*, grazer density) is gradual when fire is modelled spatially explicitly. Finally, we found that the results based on the model with spatially explicit fire are sensitive to the initial spatial distribution of the vegetation. We hypothesise that the destructive effect of fire on trees is larger when grass patches are larger because the probability of the fire spreading is larger. We conclude that for understanding the stability of ecosystems and predicting sudden shifts, understanding the interaction between the scale of spatially explicit processes and spatial distribution is crucial.

Keywords: *alternative stable states; regime shift; herbivory; spatial model; model initialisation; savanna; fire.*

Introduction

Shifts in ecosystem states and properties have been subject to research in the past decades as a result of actual abrupt changes occurring in ecosystems worldwide (Scheffer *et al.* 2001, Rietkerk *et al.* 2004, Van Nes & Scheffer 2005). Theory suggests that ecosystems can shift from one stable state into another under certain environmental conditions, *i.e.*, these systems display alternative stable states. Triggers for these shifts can be gradual changes in environmental conditions or disturbance events (Scheffer *et al.* 2001). As these shifts are often considered to be undesirable, being able to explain and predict these shifts has become an important topic in ecology (Van de Koppel *et al.* 1997, Scheffer *et al.* 2001, Rietkerk *et al.* 2004). Determining the range of environmental conditions where such alternative stable states can occur, and where the system is thus vulnerable to sudden shifts, is therefore important. Although this importance has been recognized, disregard of spatial processes and their scale in analysing this behaviour has been common (Van Nes & Scheffer 2005).

To elucidate the role of spatial processes as moderators of ecosystem stability, we investigated the effect of fire as a spatially explicit process and the scale at which fires occur on the stability of savanna ecosystems. Savannas are defined as tropical grassland systems with a discontinuous layer of trees. In general terms, three states can be defined: savanna grassland (grass dominance), pure savanna (tree-grass co-occurrence) and savanna woodland (tree dominance, Sankaran *et al.* 2005). These savanna systems are prone to sudden shifts. For example, in many savannas sudden shifts from tree-grass co-occurrence to dominance of woody cover have occurred, *i.e.*, bush encroachment (Brown & Carter 1998, Roques *et al.* 2001, Briggs *et al.* 2002). The opposite transition from a woody dominated to grass dominated ecosystem also has been reported (Dublin *et al.* 1990).

Ecosystems seem to require positive feedback mechanisms to be able to display catastrophic shift dynamics. In savannas, fire can cause such a positive feedback (Van Langevelde *et al.* 2003). This feedback is based on the positive relation between fire intensity and fuel load. In savannas, grass is the prime fuel load and the main carrier of fire. The degree to which grass is negatively affected by fire is generally limited, depending on post-fire growth conditions, as grass generally burns when in senescence. Trees on the other hand are much more affected by fires, the degree depending on fire intensity in particular (De Ronde *et al.* 2004). When fires are intense, tree damage is high, thus directing competition in favour of grass. More grass and accordingly more fuel load results in even more intense fires, causing even more tree damage, *etc*.

Fire is a spatially explicit process because the size of the burned area is variable. The scale of fire might depend on factors such as wind speed, heterogeneity of the vegetation and relative humidity. Also, the likelihood of a location catching fire is not only dependent on its own fuel load but also on the fuel load of locations in the vicinity. We investigate the effects of the spatial scale of fire on the stability of savanna ecosystems. Using a simulation model, we analyse whether the range of environmental conditions where alternative stable states occur changes when fire is modelled as a spatially explicit process at different spatial scales.

Table 7.1 Overview of the variables and parameters used in the model. Most parameter values are taken from Van Langevelde *et al.* (2003), and references therein. Rate of spread was taken from Berjak and Hearne (2002). Diffusion parameters were not based on actual field data but tuned to ensure that no undesired model behaviour would occur (*e.g.*, exorbitant high biomass values due to too large diffusion coefficients).

	Interpretation	Units	Values
H	Grass biomass	g m^{-2}	0-400
W	Woody biomass	g m^{-2}	0-1000
r_H	Water use efficiency of grasses	g mm^{-1}	1.0
r_W	Water use efficiency of trees	g mm^{-1}	0.5
θ_H	Rate of water uptake per unit grass biomass	mm yr^{-1} g^{-1}	0.9
θ_W	Rate of water uptake per unit woody biomass	mm yr^{-1} g^{-1}	0.5
d_H	Specific loss of grass biomass due to senescence	yr^{-1}	0.9
d_W	Specific loss of woody biomass due to senescence	yr^{-1}	0.4
c_H	Consumption coefficient of grass biomass by grazers	m^{2} g^{-1} yr^{-1}	0.02
c_W	Consumption coefficient of woody biomass by browsers	m^{2} g^{-1} yr^{-1}	0.02
k_H	Specific loss of grass biomass due to fire	yr^{-1}	0.1
k_W	Specific loss of woody biomass due to fire expressed per unit of energy	W^{-1}	0.01
n	Frequency of fire per year	yr^{-1}	0 or 1
a	Coefficient for the increase in fire intensity with grass biomass	W m^{-1} g^{-1}	0.5
α	Proportion of excess water that percolates to sub soil layer	-	0.4
β	Soil moisture content in the top soil layer above which water starts to percolate to the sub soil layer	mm	200-500
w_{in}	Annual amount of infiltrated water	mm m^{-2} yr^{-1}	0-1000
w_t	Available amount of water in the top soil layer	mm m^{-2} yr^{-1}	0-500
w_s	Available amount of water in the sub soil layer	mm m^{-2} yr^{-1}	0-1000
G	Grazer density	g m^{-2}	0-30
B	Browser density	g m^{-2}	0-15
D_{maxH}	Maximum dispersion rate for grasses	t^{-1}	0.025
D_{maxW}	Maximum dispersion rate for trees	t^{-1}	0.00125
K_H	Amount of woody biomass where dispersion rate of grasses is half of its maximum	g m^{-2}	300
K_W	Amount of grass biomass where dispersion rate of trees is half of its maximum	g m^{-2}	50
L	Length of cells in the lattice	m	5
R	Rate of spread of heat at location (i,j)	m s^{-1}	0-3
M_{max}	Maximum duration of burning per fire	s	25-50
$S_{i,j}$	Accumulation of heat released in neighbouring locations over M_{max} expressed as a fraction of the heat needed to ignite the vegetation (see Berjak & Hearne 2002 for a more detailed explanation)	-	0-1
S_{max}	Threshold value at which the accumulated heat causes the fuel to ignite	-	1

Model

We conducted model simulations of savanna ecosystems based on the model described by Van Langevelde *et al.* (2003). We used the main differential equations from their non-spatial model as the basis of our spatial model. We first analysed the model with fire as a non-spatially explicit process (referred to as "non-spatial"). Then, we made fire a spatially explicit process and investigated it at a small spatial scale (referred to as "small-scale fire"). Finally, we increased the spatial scale of fire (referred to as "large-scale fire").

Vegetation growth

The change in the grass component of the vegetation is formulated as:

$$\frac{dH}{dt} = r_H w_t H \frac{\theta_H}{\theta_H H + \theta_W W + w_s} - d_H H - c_H G H - k_H n H \tag{1}$$

and the woody component of the vegetation as:

$$\frac{dW}{dt} = r_W \left[w_t W \frac{\theta_W}{\theta_H H + \theta_W W + w_s} + w_s \right] - d_W W - c_W B W - k_W n a H W \tag{2}$$

The symbols, interpretation, units and values of all parameters and variables are listed in Table 7.1. Time steps in the model are in years. The equations contain 4 parts, two of which will be described in more detail below.

For both woody and grass vegetation, an increase in biomass as a function of water availability is given as (after Walker & Noy-Meir 1982):

$$r_H w_t H \frac{\theta_H}{\theta_H H + \theta_W W + w_s} \quad \text{and} \quad r_W \left[w_t W \frac{\theta_W}{\theta_H H + \theta_W W + w_s} + w_s \right]$$

Grasses only have access to water available in the top soil layer (w_t), and are competing with woody species for water in this stratum. Woody species also have access to the sub soil layer (w_s), and therefore have an advantage if sufficient rainfall allows infiltration of water to these sub soil layers. This implementation of water redistribution among trees and grasses is commonly known as the two-layer hypothesis (Walker & Noy-Meir 1982, Walter 1971), and accounts for the co-existence of trees and grasses in the model. Whether this assumption is realistic needs to be further investigated (Scholes & Archer 1997, Schenk & Jackson 2002, Van Langevelde *et al.* 2003).

The amount of water in both sub soil (w_s) and top soil (w_t) is a function of the amount of infiltrated water (w_{in}) and the water retention capacity of the top soil layer, which is expressed as:

$$\begin{aligned} w_s &= \alpha(w_{in} - \beta) && |w_{in} > \beta \\ w_s &= 0 && |w_{in} \leq \beta \end{aligned} \tag{3}$$

and

$$w_t = w_{in} - w_s \tag{4}$$

in which β is the soil moisture content in the top soil layer above which water starts to percolate to the sub soil layer (the water retention capacity), and α is the proportion of excess water that percolates to the sub soil layer.

The last term in Equation 1 and Equation 2 refers to biomass loss due to fire. The loss of woody biomass due to fire is taken to be a function of the amount of grass biomass present, where a positive relation between grass biomass availability, fire intensity and loss of woody biomass is assumed (Higgins *et al.* 2000). This formulation causes the positive feedback between grass biomass and fire, as shown in Van Langevelde *et al.* (2003).

We converted this model into a spatially explicit model by applying it to a lattice consisting of cells with a size of 25 m^2 (5 x 5 m), assuming that a mature savanna tree canopy fits in such cells. We aimed at simulating on a lattice with a spatial extent large enough to avoid edge effects, while on the other hand keeping the calculation time manageable. We found a reasonable compromise with a lattice extent of 300 by 300 cells. The simulated area is homogeneous in incoming water and no slope is assumed. Each cell of the lattice can contain both grass and woody biomass. Plant dispersion was made spatially explicitly through the application of diffusion equations, and fire was made spatially active by including an adjusted version of the fire spread model by Berjak and Hearne (2002). A description of these two processes follows.

Dispersion of plants

Plant dispersion is included in the model to allow plants to (re)colonize empty patches. Empty patches can occur in the system because they were either empty at the onset of the simulation, or because one of the two life forms is outcompeted by the other. Plant dispersion is simulated by a simple diffusion process. Dispersion of seeds is taken as very small quantities of biomass that move from one location to the next and can be described with:

$$\frac{\delta B_{i,j}}{\delta t} = D\left(B_{x,y} - B_{i,j}\right) \tag{5}$$

in which *D* is the dispersion rate (Cain 1990, Rietkerk *et al.* 2002), and sub scripts stand for different locations. In ecological systems, it can be argued that the dispersion rate decreases once other competing species are present at the location to which it is dispersed. Therefore the dispersion rate (*D*) in our model is not a constant, but decreases as a function of the presence of competitors (the other functional plant group) in a location according to:

$$D = D_{\max}\left(\frac{K_c}{K_c + B_c}\right) \tag{6}$$

where D_{max} is the maximum dispersion rate of the species in absence of the competitor, K_c is the amount of biomass of the competitor at which *D* is half of D_{max} and B_c is the amount of biomass of the competitor present at the location to which it is diffused. Because it is difficult for saplings to settle in dense swards of grasses (Loth *et al.* 2005), while tree presence can have a neutral to even a positive effect on grass growth (Belsky 1994, Ludwig *et al.* 2004), the decline in dispersion rate for trees is modelled more steeply than for grasses (see K_H and K_W in Table 7.1).

The dispersion terms are added to the initial model equations (Equation 1 and Equation 2) to generate the equations as they are used in this study:

$$\begin{aligned}\frac{dH_{i,j}}{dt} = {} & r_H w_t H_{i,j} \frac{\theta_H}{\theta_H H_{i,j} + \theta_W W_{i,j} + w_s} - d_H H_{i.j} - c_H G H_{i,j} - k_H n H_{i,j} + \\ & D_{\max H}\left(\frac{K_H}{K_H + W_{x,y}}\right)\left(H_{x,y} - H_{i,j}\right)\end{aligned} \tag{7}$$

$$\frac{dW_{i,j}}{dt} = r_W\left[w_t W_{i,j}\frac{\theta_W}{\theta_H H_{i,j} + \theta_W W_{i,j} + w_s} + w_s\right] - d_W W_{i,j} - c_W B W_{i,j} - k_W n a H_{i,j} W_{i,j} + D_{\max W}\left(\frac{K_W}{K_W + H_{x,y}}\right)\left(W_{x,y} - W_{i,j}\right) \qquad (8)$$

These equations describe the dynamics of plant biomass at a location both as a function of growth, mortality and competition, as well as a result of redistribution through dispersion. For each location (*i,j*), dispersion of plants from or to a location (*x,y*) is taken into account, where (*x,y*) is the average over the four direct neighbours of (*i,j*).

Fire spread

Fire spreads in a chain reaction as locations combust as a result of neighbouring locations releasing heat. The combustion process can be split into three phases (Brown & Davis 1973, Trollope 1998). First, there is preheating where the temperature of fuel ahead of the fire is driven to its ignition point and the release of flammable hydrocarbon gasses is initiated. Second, these gasses ignite, resulting in flaming combustion. Finally, solid fuel is consumed through glowing combustion. To model the spread of fire, two variables are needed: the accumulation of heat ($S_{i,j}$) at a location (*i,j*) as a result of heat influx from neighbouring locations, and the threshold value (S_{max}) at which the accumulated heat causes the fuel to ignite into flaming combustion. After ignition, the location under consideration starts emitting heat as well, causing heat accumulation in unaffected neighbouring locations, and so on.

The influx of heat from one location to the other is a local cellular automaton rule (adjusted from Berjak & Hearne 2002):

$$S_{i,j} = \sum_{M=1}^{M_{\max}}\left[\frac{1}{L}\left(R_{i-1,j} + R_{i,j-1} + R_{i+1,j} + R_{i,j+1}\right) + \frac{0.17}{L\sqrt{2}}\left(R_{i-1,j-1} + R_{i-1,j+1} + R_{i+1,j-1} + R_{i+1,j+1}\right)\right] \qquad (9)$$

in which $S_{i,j}$ is the accumulation of heat released in neighbouring. Location (*i,j*) burns when $S_{i,j} > S_{max}$ and does not burn when $S_{i,j} \leq S_{max}$. When a location is burning, *n* is set to 1 (Equation 1 and Equation 2), else $n=0$. Also, when a location is burning, it starts emitting heat to neighbouring cells (*i.e.*, *R* gets a positive value) otherwise it does not. *L* is the length of the locations in the lattice and $R_{i,j}$ is the rate of spread of heat which is correlated with biological (*e.g.*, fuel availability) and abiotic (*e.g.*, wind speed) determinants (Rothermel 1972, Bond & Van Wilgen 1996). In our model, $R_{i,j}$ is kept at a constant positive rate in case grass is present and set at 0 if not. Fire is simulated in the model in a subroutine with time steps of seconds that is repeated each year.

The maximum time fire can spread throughout the landscape is set with M_{max}. After M_{max} seconds, the spread of fire stops and the change in woody and grass biomass is calculated (Equation 7 and Equation 8). There can be several causes for the extinction of a fire, such as lack of fuel (*e.g.*, due to extensive grazing or previous burning), low flammability of the fuel (*e.g.*, with a very high water content), a drop in ambient temperature below a critical temperature, or high relative humidity (Bond & Van Wilgen 1996). In our approach, once ignited, cells will continue to emit heat until M_{max} is reached. This implies that cells earlier ignited in the burning routine will emit heat longer than cells later on. This can affect fire spreading behaviour when the threshold value for combustion (S_{max}) is modelled as a function of fuel condition (*e.g.*, moisture content of the fuel). Then longer emitting of heat could ignite fuel that would otherwise not ignite. However, because we keep the S_{max} constant for cells with fuel present for simplicity reasons, we experience no effects from specifying M_{max} as a landscape parameter rather than as a parameter for each cell (as is the case in the original model of Berjak & Hearne 2002).

During each simulation step of a year, a pre-set number of ignition events take place. Locations are randomly chosen for these ignition events, where locations with a high fuel load have a greater chance of being selected than locations with a low fuel load. Once all ignition events have taken place, fire starts spreading from the ignited locations to neighbouring locations as described by Equation 9. Using this routine, the area that burns each year can be controlled and locations with a lot of grass biomass have a higher chance of igniting.

Model analyses

First, we analysed the "non-spatial" model where all locations have the same probability of receiving an ignition event. Second, fire was treated as spatially explicitly ("small-scale fire" and "large-scale fire") and the size of the area burned was controlled (using M_{max}). In the "small-scale fire" analysis, M_{max}=25 s (small area burned), and in the "large-scale fire" analysis, M_{max}=50 s (large area burned). Fire frequency in the "non-spatial" analysis is based on the probability of a location receiving an ignition event. In the "small-scale fire" and "large-scale fire" analyses, however, fire frequency is calculated as the proportion of the area that burns each year. For the "non-spatial" analysis, for example, a fire frequency of 0.5 means that each location has a 50% probability of catching fire in each time step of one year. For the analysis with the spatially explicit fire, this would mean that on average each year half of the area burns. To obtain equal frequencies in both the "small-scale fire" and "large-scale fire" analyses, different numbers of ignition events were used. In case of the "small-scale fire" analysis, many small fires were ignited, in case of the "large-scale fire" analysis, a few large fires were ignited. In these analyses, owing to the chances of fires going extinct, the realized fire frequency can be lower than the pre-set fire frequency. To compare the different analyses, we kept the realised fire frequency constant.

We analysed two series of simulations. Each simulation lasted up to maximally 1000 time steps but was stopped when all the variables reached an equilibrium. In the first series, we investigated which ecosystem state can be expected when water availability (w_{in}, Equation 1 and Equation 2, Table 7.1) and soil type (*i.e.*, water retention capacity β, Equation 1 and Equation 2, Table 7.1) are given. In these simulations, we also varied grazer density (G) and fire frequency (n). For this series, each simulation was performed with random initial vegetation distribution maps, but with different initial vegetation abundances, allowing combinations of high and low cover and abundances of grass and woody biomass: varying from high grass cover (90%) and low wood cover (10%) with low biomass (1 g m^{-2}), low grass cover (10%) and high wood cover (90%) with low biomass, high grass cover (90%) and low wood cover (10%) with high biomass (1000 g m^{-2}), and low grass cover (10%) and high wood cover (90%) with high biomass (1000 g m^{-2}).

In the second series, we investigated the effect of differences in the initial sizes and number of grass patches (*i.e.*, adjacent cells with low woody biomass and high grass biomass), keeping overall grass cover constant, as fire can only be ignited in locations containing sufficient fuel load and the scale of fire depends on the neighbouring locations having sufficient fuel load. The spatial configuration was varied along a gradient of many small patches to a few large patches.

To interpret the results of simulations, a simple classification scheme was used. If the average biomass of either grass or trees was below 1 g m^{-2}, it was considered to be not present. This allowed us to distinguish between grassland (grass biomass > 1g m^{-2} and tree biomass < 1g m^{-2}), savanna (both grass and tree biomass > 1g m^{-2}), woodland (tree biomass > 1g m^{-2} and grass biomass < 1g m^{-2}), and alternative stable states where, given the initial vegetation distribution, either woodland or savanna is the stable state at the end of the simulation.

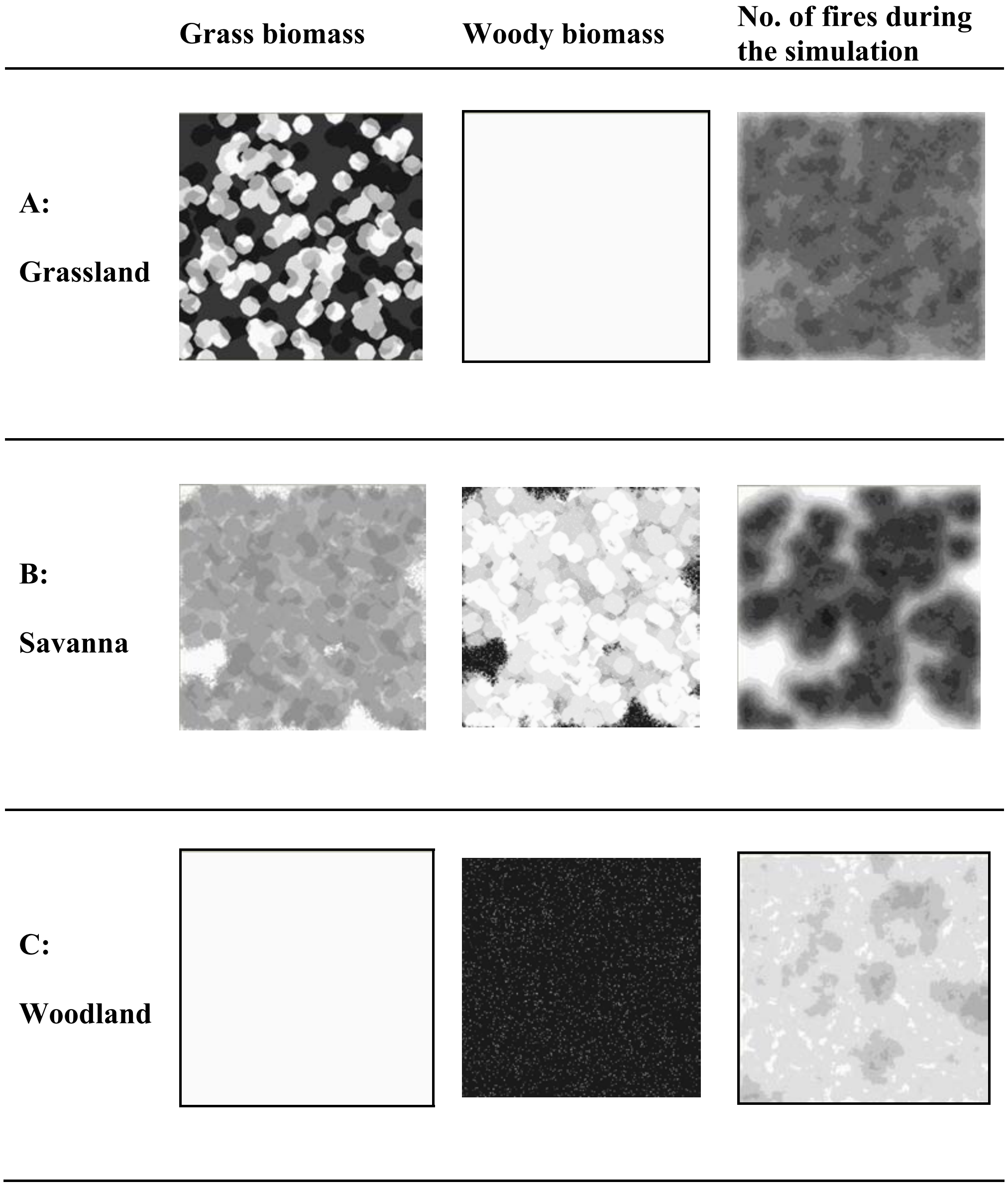


Figure 7.1 Three simulation results. Each simulation provides a "map" with grass biomass, woody biomass and the number of fires that occurred in each location. Based on the classification scheme explained in the text, each simulation could be either classified as (A) grassland, (B) savanna or (C) woodland. Dark colours indicate high values and light colours indicate low values.

Results

Non-spatial versus spatial model

The effect of the spatially explicit spread of fire is illustrated in Figure 7.1. If environmental conditions lead to the formation of grassland (Figure 7.1A), the distribution of grasses is heterogeneous, due to burning. In the case of savannas (Figure 7.1B), a heterogeneous mixture of grasses and trees is the result. Conversely, the presence of woodland (Figure 7.1C) indicates that burning has hardly any effect, as there are no grasses, leading to a spatially homogeneous cover of trees. The number of times a location burned during the simulation is illustrated in the panes on the right-hand side of Figure 7.1. Because the initial amount of grass biomass in these three simulations was equal, burning occurred initially in the simulation that resulted in woodland (Figure 7.1C).

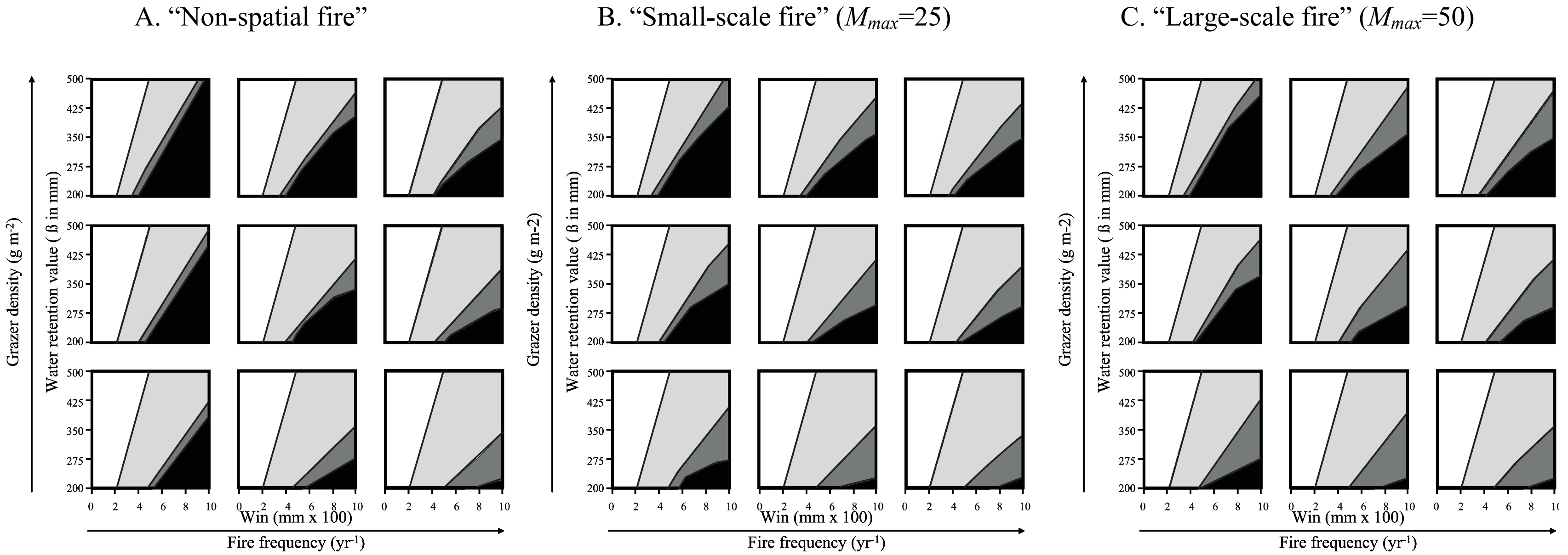
For the first simulations series, parameter planes show the response of the modelled ecosystem to the amount of infiltrated water (w_{in}) and soil properties (water retention capacity β) (Figure 7.2). Each plane shows that the system changes from grassland to savanna to woodland with increasing water infiltration (W_{in}, x-axis) and under certain conditions the system can switch between savanna and woodland (*i.e.*, alternative stable states occur). An increase in the water retention capacity of the soil (β, y-axis) shows an inverse trend. Considering the two-layer hypothesis (Equation 1 and Equation 2) built into the model, the relative advantage of trees to grasses decreases as less water percolates to deeper layers. Therefore, soils with higher water retention values of the top soil provide less favourable conditions for woody species. This concurs with findings by Van Langevelde *et al.* (2003).

An increase in fire frequency increases the range of abiotic conditions (w_{in} and β) where savannas as well as alternative stable states can be found (Figure 7.2) as fire triggers the positive feedback between grass biomass and fire intensity (Van Langevelde *et al.* 2003). Increasing grazer density reduces the grass biomass, and therefore favours trees. Simulations with higher grazer density allow woodland to occur under abiotic conditions that would otherwise support savannas (Figure 7.2).

Effect of spatially explicit fire and its scale

To compare the different model analyses, Figure 7.3 gives the fraction of the parameter planes depicted in Figure 7.2 occupied with the different ecosystem states. When fire is included as spatially explicit process (*i.e.*, comparing the “non-spatial” analysis with “small-scale fire” analysis), the results show a general trend towards an increase in the occurrence of alternative stable states (Figure 7.3D, E and F). At high fire frequencies (n=1.0), the increase in the conditions where alternative stable states occur is relatively low (Figure 7.3D), and is mostly at the expense of the occurrence of savanna (Figure 7.3A). The occurrence of woodland remains relatively unchanged when fire is included as a spatially explicit process at high fire frequency (Figure 7.3G).

At intermediate fire frequency (n=0.5), the increase in occurrence of alternative stable states is more pronounced (Figure 7.3E) compared with high fire frequency (Figure 7.3 D); with “small-scale fire”, this increase is mainly at the expense of woodland (Figure 7.3H). When the scale of burning is increased (“large-scale fire”), the occurrence of woodland remains stable and a decrease in the occurrence of grassland (Figure 7.3B) results in a further increase in the occurrence of alternative stable states.



A. “Non-spatial fire”

B. “Small-scale fire” (M_{max}=25)

C. “Large-scale fire” (M_{max}=50)

Figure 7.2 Parameter planes of the model with water availability (win in mm along x-axis) and water retention capacity (β in mm along y-axis) as explaining parameters, based on the first series of simulations. Output is classified as explained in the text. Along the secondary axes, grazer density (G=5, 10 and 15 in g m-2 over rows) and fire frequency (n=0.1, 0.5 and 1 in yr-1 over columns) are represented. Other parameters are as presented in Table 7.1. Simulations are “non-spatial fire” (A), “small-scale fire” (Mmax=25, B), and “large-scale fire” (Mmax=50, C), see text for explanation.
Legend : ☐ =Grassland, ░ =Savanna, ▒ =Alternative stable states, ■ =Woodland

At low fire frequencies (*n*=0.1), the effect of the size of fire on the occurrence of alternative stable states is determined by grazer density (Figure 7.3F). At low grazer density, the conditions where alternative stable states are found increase monotonically with increasing scale of fire, while at high grazer density there is a hump-shaped response to the scale of fire (Figure 7.3). These different reactions to spatially explicit fire are related to increases and decreases in the occurrence of woodland. When fire only occurs at small scale, a general decrease in the occurrence of woodland can be seen. For large-scale fires, however, the response depends on grazer density. At high grazer density, the conditions for the occurrence of woodland are increased, while at low grazer density they remain relatively stable. As with large-scale fire (*i.e.*, a few large fires), the realised fire frequency is more dependent on the success of the fire in spreading than with more small-scale fires. This success of fire spreading is related to the abundance of grass biomass in the surroundings of an ignition event and, therefore, grazer density has a direct effect on this success. The results in Figure 7.3 suggest that the effect of grazing on the success of fire spread becomes more pronounced at lower fire frequency.

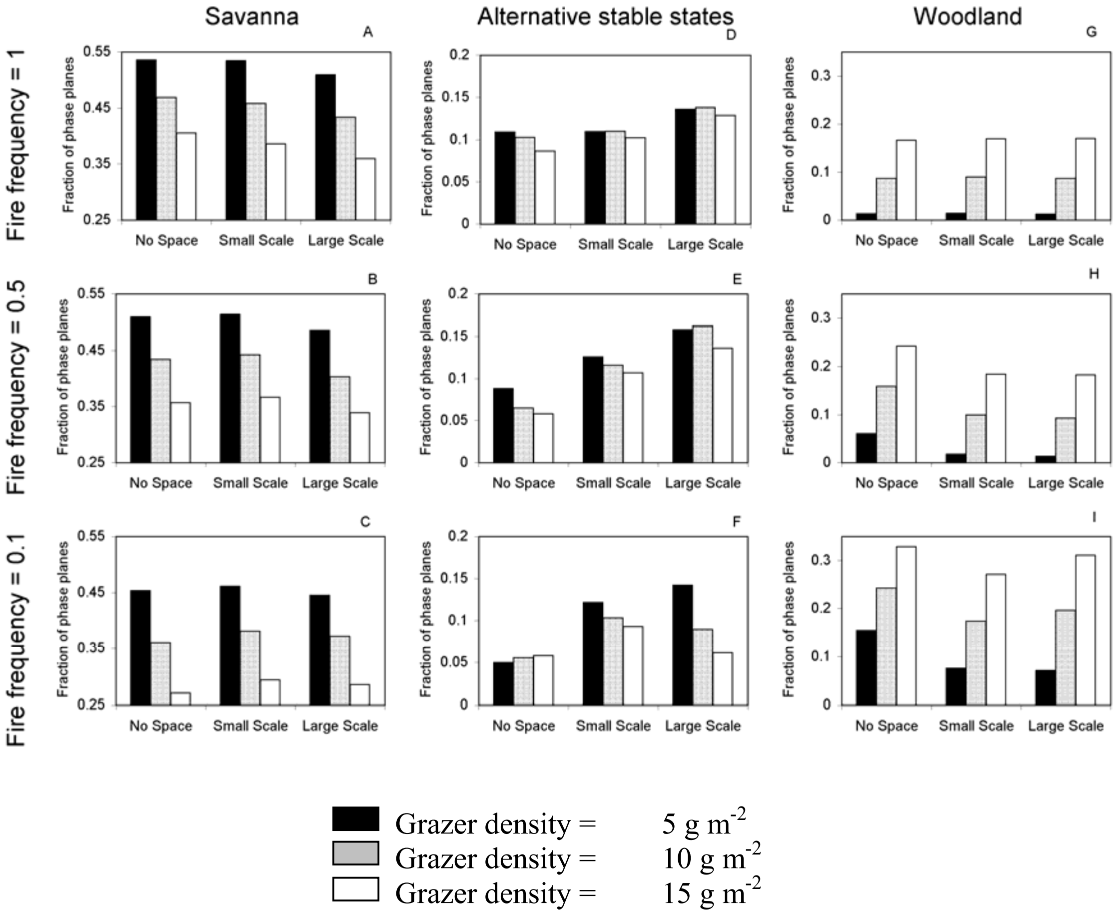


Figure 7.3 Fraction of the states in the parameter planes given in Figure 7.2. Bars represent the fraction of the parameter plane occupied by a system state. The fraction of the parameter plane occupied by grassland is not shown because grazing or fire does not affect this fraction. The different bar shadings represent grazer density and the different rows of graphs indicate different fire frequencies.

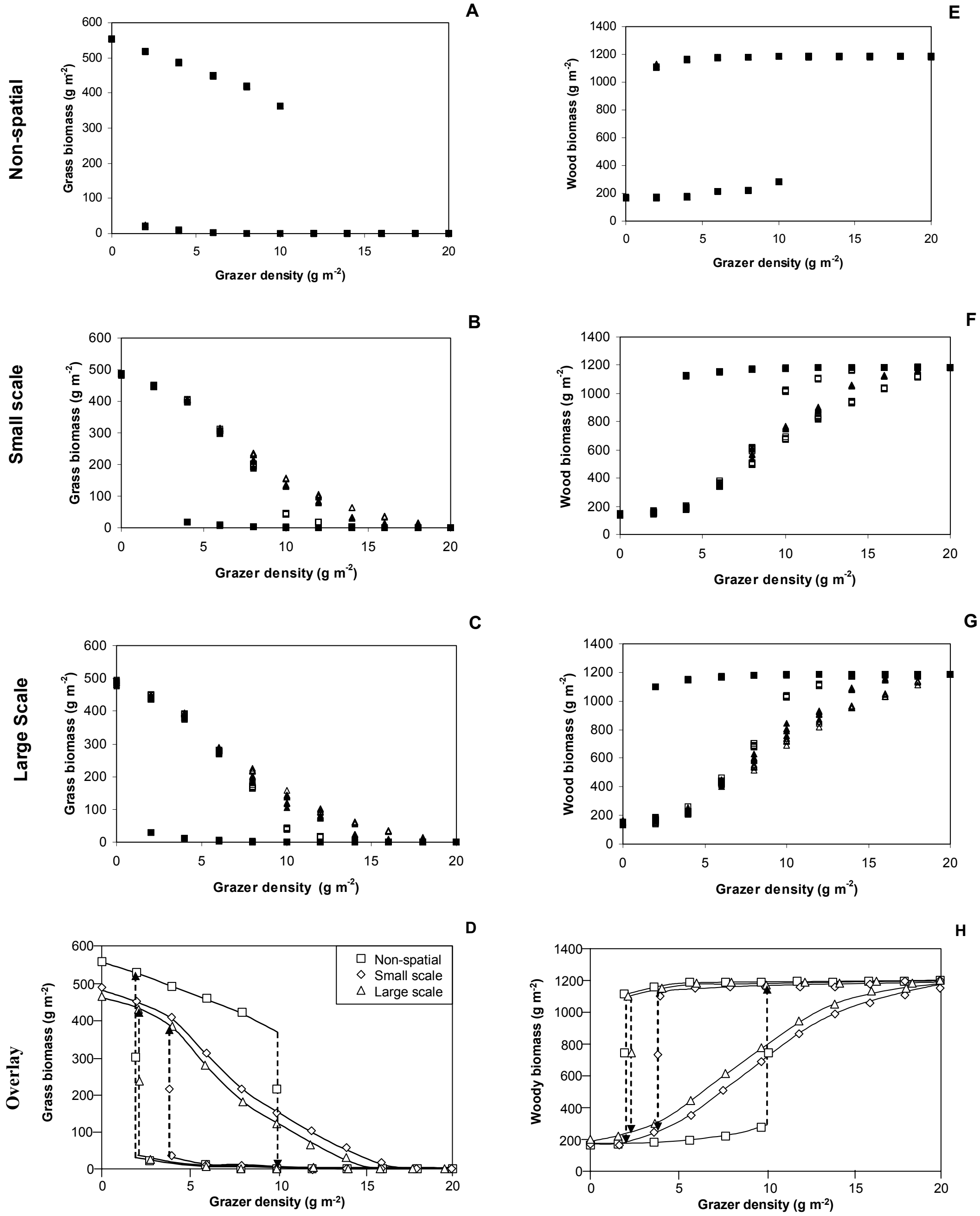


Figure 7.4 Woody (W) and grass (H) biomass (averaged over the total simulated area in g m^{-1}) as function of grazer density (g m^{-2}). Figures D & H show the average for grass and woody biomass respectively over grazer densities for all three different simulation types (*i.e.*, non-spatial, small scale and large scale). The symbols in Figures D and H represent the different analyses, and forward and backward shifts are indicated with arrows. Parameters were set as given in Table 7.1 except for B=0, w_{in}=1000, β=400, n=1.0. Different symbols indicate different initial vegetation distributions, allowing combinations of high and low cover and abundances of grass and woody biomass: ■= low grass cover (10%) and high wood cover (90%) with low biomass (1 g m^{-2}); ▲= high grass cover (90%) and low wood cover (10%) with low biomass (1 g m^{-2}); □= low grass cover (10%) and high wood cover (90%) with high biomass (1000 g m^{-2}) ; △= high grass cover (90%) and low wood cover (10%) with high biomass (1000 g m^{-2}).

Figure 7.4 gives the average tree and grass biomass as a function of grazer density. Figure 7.4 A and E (“non-spatial fire” analysis) bears a resemblance to Figure 7 in Van Langevelde *et al.* (2003). When simulating fire as a spatial process, the total equilibrium grass biomass in a savanna system (the upper equilibria) decreases (Figure 7.4B and E). The regions in which alternative stable states occur increase when simulating fire as a spatial process, as was also shown in the previous results (compare Figure 7.3D, E and F). We found that in simulations with fire as a spatial process, there is no forward catastrophic shift (increasing grazing density from savanna to woodland), although this shift is present in the non-spatial simulation. The backward catastrophic shift, however, is present in all simulations (Figure 7.4D and H).

Initial vegetation distribution

Figure 7.5 displays the result of the second series of simulations where initial vegetation distribution was varied in grass patchiness while total grass cover remained constant. We found that increasing grass patch size (and consequently fewer patches) results in a higher equilibrium value for grass biomass. Few large grass patches allow for spreading of fire over a larger area compared to a lot of small grass patches. Moreover, each small grass patch has a lower chance of becoming ignited. As burning damages trees and reduces competition with woody species, small grass patches have a higher probability of disappearing. Therefore, grasses dominate the resulting landscape, and consequently the related amount of grass biomass is lower when the landscape contains small grass patches.

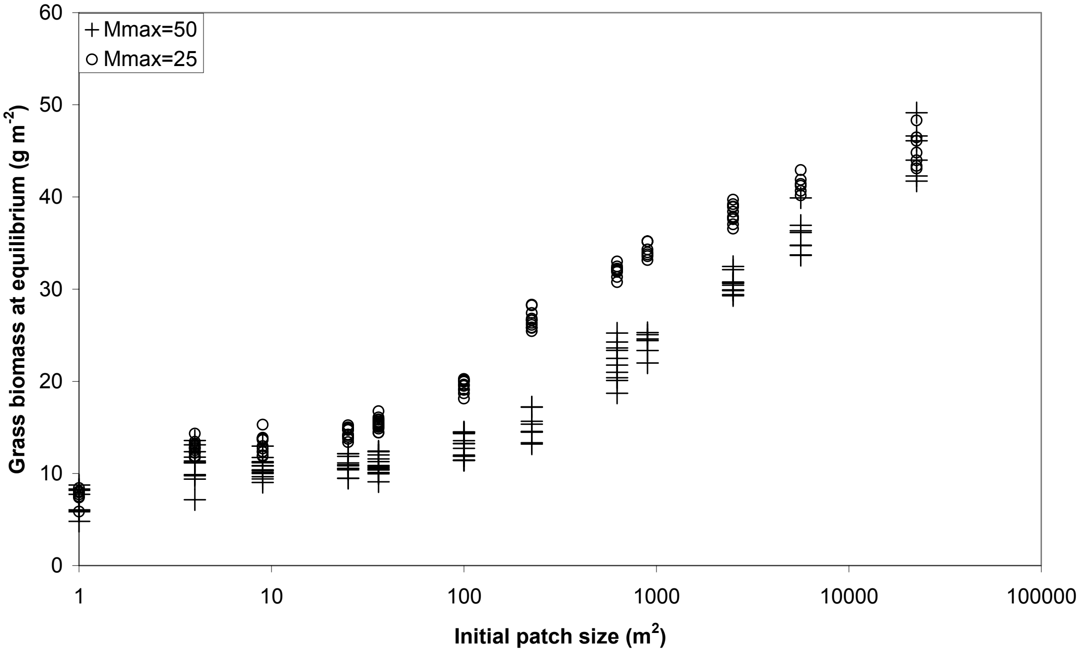


Figure 7.5 Total grass biomass of simulations with different initial vegetation distribution, *i.e.*, different size and number of grass patches keeping the total cover of grass constant. The x-axis shows the size of the grass patches. Simulations with large grass patches were initiated with fewer patches than simulations with small grass patches, yielding a similar total grass cover (25%). Two simulation series are shown: simulations with a small spatial scale (M_{max} = 25) of fire and simulations with a large spatial scale (M_{max} = 50) of fire.

The effect of the scale of fire is visible at intermediate grass patch sizes. Here, large-scale fires yield lower grass biomass than small-scale fires. When both small-scale and large-scale fires succeed in burning for the maximum time (M_{max}) in landscapes with large grass patches, they yield similar areas burned, having similar effects on grass biomass. When the size of the grass patches is smaller than the area that can be burned by a single fire within M_{max}, especially in the case of large-scale fires, the resulting area burned, and consequently the area that is dominated by grasses, diminishes. Once both small-scale and large-scale fires are equally hampered by the size of grass patches, at very small grass patch sizes, this difference disappears again.

Discussion

In this paper, we investigate the effects of the spatial scale of fire on the stability of savanna ecosystems. We showed that the range of environmental conditions (*i.e.*, rainfall and soil types) where alternative stable states can occur increases when fire is included as a spatially explicit process. When the range where alternative stable states occur increases at the expense of the conditions where otherwise only savanna would occur (*e.g.*, compare Figure 7.3B and E: the step from “small-scale” to “large-scale”), these areas become more prone to sudden shifts such as bush encroachment. Under these conditions, the ecosystem can shift from savanna to woodland. Without fire as a spatially explicit process, the model would predict that the system would always recover as savanna after disturbances. When the range where alternative stable states occur increases at the expense of woodland (*e.g.*, see Figure 7.3E and H: the step from “non-spatial” to “small-scale”), savannas could be found where otherwise only woodlands would be expected. Savannas, then, are predicted to occur under a wider range of conditions.

The spatial scale of fire is the determinant whether the environmental conditions where alternative stable states can be found, increase either at the expense of either woodland or savanna. With small-scale fires, the region with alternative stable states increases at the expense of woodland, while with large-scale fires this happens in the direction of savanna (Figure 7.4). This suggests that many small-scale fires favour savannas rather than a few large-scale fires. Many small-scale fires may have a larger negative effect on trees as fire can occur in more (isolated) patches of grass than a few large-scale fires can (Jeltsch *et al.* 1998). Although empirical evidence is lacking, this idea is gaining interest in management as small-scale burning is believed to increase diversity (Owen 1972, Brockett *et al.* 2001). This wider range of environmental conditions where alternative stable states can be found and the effect of the spatial scale of fire concur with the findings of Sankaran *et al.* (2005) who related the occurrence of savannas to environmental conditions. They showed that rainfall is a major determinant for the maximum woody cover in savannas. They suggested that fire, herbivory and soil properties interact to reduce woody cover below this maximum. However, they could not explain the variation below this maximum. We show that with fire as a spatially explicit process with varying spatial scales, large variation in woody biomass is indeed predicted under given environmental conditions (Figure 7.4H).

Figure 7.4 shows that when fire is modelled non-spatially explicitly, the ecosystem can indeed experience sudden shifts under certain conditions (Figure 7.4A, cf. Van Langevelde *et al.* 2003). Alternative stable states are also found when fire is modelled spatially explicitly (Figure 7.4B and C). With this spatially explicit fire, however, the ecosystem shows only a sudden shift with decreasing grazer density. In contrast, the system responds gradually to increasing grazer density. Van Nes and Scheffer (2005) found similar behaviour in three other models. They argued that forward and backward shifts (for our system: savanna to woodland and woodland to savanna, respectively) can be the result of different mechanisms. When the mechanism that rules the forward shift is spatially localised, the forward shift occurs on a few locations. Subsequently, there will be hardly any effect for the whole landscape.

In savanna ecosystems, an increase in grazer density does not lead to a forward shift (collapse of grass biomass) when fire is modelled spatially explicitly. This increase in grazer density leads to a decrease in grass biomass, and therefore in a decreasing probability of grass patches to become ignited. Therefore some grass patches shift to woody dominance, decreasing the total area of grass dominance. This increases the probability of ignition events on the remaining grass patches in the next time step, causing these grass patches to persist. If all patches are ignited with the same probability ("non-spatial" fire), the shift happens in all the locations at once, thus also showing this effect for the whole landscape. The absence of this forward shift results in a higher grass biomass under stressful conditions (*i.e.*, high grazer density) when fire is modelled spatially explicitly compared to the non-spatial model (Figure 7.4D, grazer density between 10 and 15 g m^{-2}). However, the opposite holds under lower grazer densities. This concurs with Van de Koppel and Rietkerk (2004). They compared a non-spatial model of arid grazing systems with a spatial one. They included the redistribution of water as spatial process. Van de Koppel and Rietkerk found that under low rainfall conditions, the spatial model showed higher grass biomass. This could be explained because in the spatial model heavily impacted patches experienced vegetation collapse and rainfall in these patches was redistributed to patches with more vegetation. Here, the vegetation could persist due to this influx of water. In the non-spatial model, this was not the case, and therefore all patches collapsed. In our study, the mechanism is similar, *i.e.*, increasing stress leads to a larger role of the spatially explicit positive feedback, but we consider the spatial effect of a disturbance rather than the redistribution of a limiting resource as in Van de Koppel and Rietkerk (2004).

For the backward shift, *i.e.*, the shift from woodland to savanna, the mechanism works differently. If grazer density is sufficiently reduced, grasses succeed in building up enough biomass to be able to catch fire, which happens everywhere (*i.e.*, over the whole landscape) and is not localised. Fires occur everywhere and suppress trees, resulting in more grass and less woody biomass until a new state is reached with grass dominance (Vila *et al.* 2001). Our results suggest that sudden shifts such as bush encroachment are less likely to occur with increasing grazer density than predicted by non-spatial models (such as Walker & Noy-Meir 1982, Van Langevelde *et al.* 2003). In contrast, a decrease in grazer density together with fire can induce sudden shifts from woody dominance to savanna (cf. Van Langevelde *et al.* 2003).

We also found that the initial size of grass patches has an effect on the results (Figure 7.5). This indicates that when working with spatial models, the found results may depend on the initial spatial distribution of the vegetation. Often with spatially explicit ecological models, random initial biomass distributions are used and no consideration is given to other possible spatial distributions of the initial biomass (Jeltsch *et al.* 1998, Van Wijk & Rodriguez-Iturbe 2002), or the emphasis is placed on the resulting self-organised pattern (Rietkerk *et al.* 2002, 2004). This implies that the role of fire depends not only on the cover of grasses, but also on its spatial distribution. We hypothesise that the destructive effect of fire on trees is larger when grass patches are larger because the probability of fire spread is larger (Peters *et al.* 2004, Breshears 2006).

For our savanna ecosystems, we conclude that an increase in the spatial scale of fire increases the range of environmental conditions where alternative stable states can occur, and thus where the system is vulnerable to sudden shifts. We further conclude that for understanding the stability of ecosystems and predicting sudden shifts, understanding the interaction between the spatial scale of spatially explicit processes and spatial distribution is crucial.

Acknowledgements

We would like to thank M. Scheffer, E. van Nes and H. Prins for valuable input to draft versions of the manuscript. E. Tynan reviewed the manuscript on English.

CHAPTER 8
Synthesis: the effects of spatial patterns & processes

The main aim of this thesis was to investigate the effects of spatial processes and heterogeneity on sudden shifts in ecosystems. I identified spatial processes as potential causes of spatial heterogeneity. Also, the results from my models suggested that spatial heterogeneity can reduce the probability of sudden shifts in ecosystems. When a system is spatially heterogeneous, the probability that sudden shifts will occur everywhere simultaneous is less. This does not mean that sudden shifts do not occur on a local scale, however. But the heterogeneity in the system at a larger regional scale buffers these small local shifts. In this thesis I presented seven studies that investigated this process. In this last chapter, I discuss the steps that led to the final conclusion by zooming in on relevant issues of the previous chapters. I then proceed to generalize these findings, derived from a study of a savanna, to a broader ecological context, and identify gaps that still need further investigation. After that, I discuss the implications for the management of savanna ecosystems, with special reference to the problem of bush encroachment.

The interaction between spatial patterns and processes

Three research questions have guided this study from the start:
1-"What is the effect of spatial heterogeneity on spatial processes?"
2-"How is spatial heterogeneity created by spatial processes?" and
3-"Is the occurrence of sudden ecosystem shifts influenced by these spatial patterns and processes?"
I investigated these using a range of techniques, including empirical data analysis and modelling. The results are presented in this thesis as six studies (Chapters 2-7), each of which addressed parts of these questions.

I used a savanna as the model ecosystem, a logical choice for several reasons. First, savannas are spatially and temporally highly variable (chapter 2, Scholes & Archer 1997). Second, they are subject to many spatially explicit processes like fire (Carmona-Moreno *et al.* 2005, Bond & Keeley 2005) and herbivory (Dublin *et al.* 1990, Prins & Van der Jeugd 1993). Third, savannas can undergo rapid changes in structure and composition (*i.e.*, catastrophic shifts such as bush encroachment: Archer *et al.* 1988, Briggs *et al.* 2002, Brown & Carter 1998, Roques *et al.* 2001, Van Auken 2000). Lastly, savannas are expected to be especially sensitive to future land use and climatic changes (Sala *et al.* 2000, Bond *et al.* 2003). Assessing their stability is therefore important to predict the likelihood of future ecosystem shifts.

Fire

In an explorative analysis of aerial photographs I found that savannas are indeed highly variable in their physiognomy and that tree patterns correlate more strongly with top-down factors — factors that potentially reduce tree biomass — than they do with bottom-up factors — factors that potentially influence the growth of trees (chapter 2). Within the set of top-down factors distinguished in this study, I found that fire occurrence correlated with nearest neighbour distances in trees, while the presence of sheep and goats and fire occurrence correlated with the size of tree clusters.

In the experimental burning plots of the Kruger National Park, South Africa, I investigated this relation between fire and nearest neighbour distances empirically

(chapter 3). The results suggest that the spatial organisation of trees in savannas can affect the fire damage they experience. Trees in close proximity to one another suffer less from fire than trees further apart. In addition, fires also affect the spatial organisation of trees as it appears to stimulate the formation of monospecific clusters on clay soils. In clustered patterns, trees are in closer proximity to each other than can be expected on the basis of a random distribution. The damaging effect of fire on trees in these clusters might become less, when trees can protect each other against fire. This would increase the performance of trees in clusters over solitary trees. Living in a cluster, however, comes at a cost, as competition for resources is stronger. Therefore a clumped distribution can be more predominant on fertile (clay) soils than on more poor (sandy) soils

Spatial heterogeneity can intensify interactions among individuals that would otherwise be less strong (Tilman *et al.* 1997, Bergström *et al.* 2006). Interactions that have often been investigated in a spatial context are competition and facilitation. Interesting examples of facilitation are unpalatable plants that protect more palatable plants from grazing (Smit *et al*. 2006, Carrick 2003) or settled shrubs that offer a refuge from high irradiation levels for new saplings (Holmgren *et al*. 1997). Also protection against fire can be one of those facilitative effects that are influenced by the spatial organisation of plants.

Herbivores

Next to fire, I looked at the effect of herbivory on spatial heterogeneity. I performed two modelling studies in which I investigated the effects of different spatial behaviour of herbivores on the formation of spatial pattern.

In the first study, I assumed that herbivore densities were constant, and that herbivores had complete knowledge of the area (chapter 4). I modelled patch selection in a grid environment, based on the attractiveness of each cell. Attractiveness of a cell in the model was based on the amount of forage available in the cell, and the quality of the forage. I found that herbivores can create spatial patterns only when they forage "spatially dependent", and when foraging induces "self facilitation". Self facilitation was defined as the process where removal of forage by herbivory increases the quality of the forage in following time steps. Spatially dependent foraging means than when herbivores forage on a selected patch, they do not only forage in that specific patch, but also consume vegetation in the immediately surrounding patches which can be potentially less attractive. The study suggested that at intermediate levels of herbivory, spatial heterogeneity could be induced, while at higher or lower levels of herbivory, heterogeneity would be reduced.

In the following study (chapter 5), I relaxed the assumptions of complete knowledge of the environment by herbivores, as well as the assumption of fixed herbivore densities. I formulated a Gierer-Meinhardt like model (Gierer 1981, Meinhardt 2003), where the distribution of herbivore pressure (both grazing and browsing) was a function of available forage (both grass and tree biomass). I found, using Turing stability analysis, that the spatial distribution of herbivore pressure can create spatially heterogeneous vegetation patterns without self-facilitation, but with spatially dependant grazing. Herbivore pressure was highest in patches with high forage availability, but also in areas surrounding patches with high forage availability. In this way both grazers and browsers facilitated each other indirectly. For example, browsers forage heavily on patches with high tree (leaf) biomass, but in the mean time also suppress tree biomass in surrounding areas where less tree biomass is available. In these surrounding areas grass biomass then will be able to perform better due to less competition with tree biomass. Grazers in their turn benefit from this enhanced grass production.

The studies in this section discussed how interactions between patterns and spatial processes can operate. The results show that under certain conditions, both herbivores (chapters 4 and 5) and fire (chapter 3) can increase and maintain heterogeneity in the system. Also, results imply that spatial heterogeneity affect the processes. Fires are less effective in situations where nearest neighbour distances are small, while grazers and browsers can indirectly facilitate each other through the presence of patterns (chapter 5).

Heterogeneity and tree-grass dynamics

In the previous section I discussed how interactions between spatial processes like burning and herbivory and spatial patterns in savannas can operate. The next step is to investigate how these interactions affect the stability of savannas. I investigated the effect of the spreading of fires on savanna stability and the occurrence of ecosystem shifts.

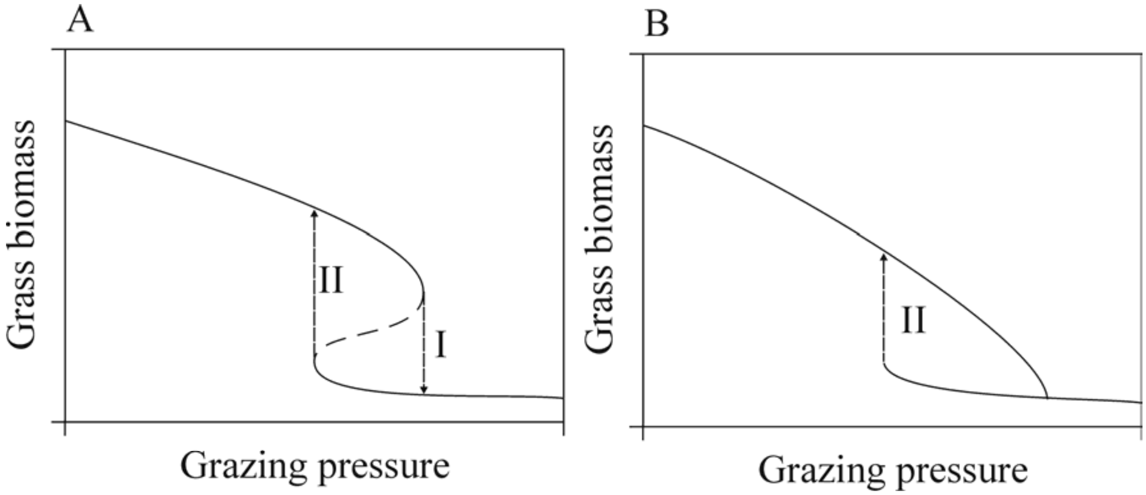


Figure 8.1 The effect of spatial heterogeneity on the occurrence of catastrophic shifts. When modelled without spatial processes (A) systems that display catastrophic behaviour, can show both forward (arrow I) and backward (arrow II) shifts. When this same system is analysed with spatial processes (B) one of the shifts can disappear. Notice that the ecosystem response may be in general lower in a system with spatial interactions compared to a system with no spatial interactions

To analyse the effect of spatially explicit burning on the occurrence of ecosystem shifts and the stability of the savanna ecosystem, I formulated a model where fire was included as a spatial process(chapter 7). Savanna fires were modelled spreading from randomly located ignition points. The spreading of fire was assumed to be a function of the amount of grass biomass present in locations that the fire was spreading towards. I varied the scale of fires, by varying the time that fires could spread through the simulated landscape. I also performed simulations, where fires were not spreading through the landscape. Here fires were applied as a blanket—each location was forced to burn, irrespective of the amount of grass biomass present. Simulating fire as a spatial process increased the range of environmental conditions where alternative stable states can occur. Results also suggest that some shifts disappear and are replaced by more gradual responses of the ecosystem, while other shifts remain in the system. In chapter 7 I discussed in detail what the effect of different scales of fire were on the occurrence of alternative stable states. Here, I expand on the disappearance of some of the ecosystem shifts, and their consequences in broader ecological terms.

In chapter 7 I compared results of simulations with spatial and non-spatial implementations of the same model which were ran with different initial densities of grass biomass, and with different densities of grazers. Figure 7.4 shows the equilibrium grass densities against the densities of grazers and the results suggested for the spatial and non-spatial models responses comparable to those presented in Figure 8.1. In the non-spatial model the system seemed to respond with a classical catastrophe fold to increasing stress (Figure 8.1A) in which both a forward shift (arrow I) and a backward shift (arrow II) could occur. The spatial model however shows a less familiar response (Figure 8.1B) in which only the backward shift remained.

The loss of the forward shift must be related to the spatial processes that take place in the model, because for the rest, the two models are identical. In the model, fire is a source of spatial heterogeneity. It has an effect on the tree grass ratio in randomly selected patches that are ignited. In burned patches, grasses perform better than in unburned patches. When conditions favour grass dominance — *e.g.*, at low levels of grazer density — burning does not introduce spatial heterogeneity in the sense that some patches contain both trees and grasses while others patches contain only trees, *all* patches contain both trees and grass. If conditions become less favourable for grass — *e.g.*, when grazers become more abundant — grass needs the positive effect that burning has on their performance, and grass only remains in patches that are frequently burned, while other patches lose their grasses. Then fire introduces spatial heterogeneity.

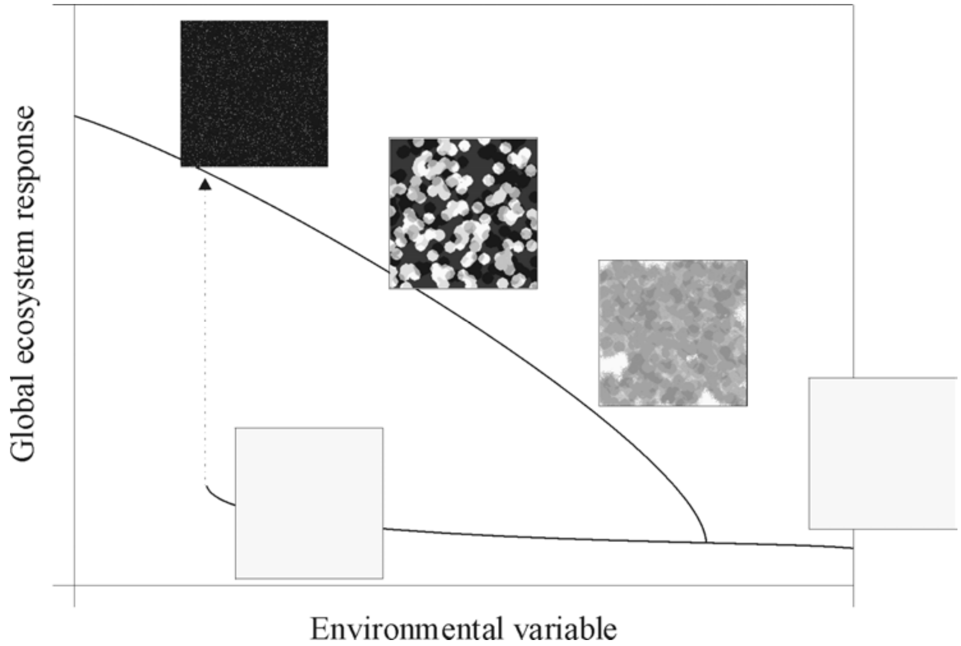


Figure 8.2 Graphical representation of how shifts in one direction can become gradual on a global level, while a shift in the opposite direction is sudden on a global level.

I propose that this spatial heterogeneity is the main reason why the forward shift disappears, while the backward shift remains (Figure 8.2). Fire is able to introduce spatial heterogeneity in a savanna system under certain levels of grazer densities. Then as grazer density increases, some patches lose their grasses, and become tree dominated. Basically, in these patches, a forward shift occurs. At the level of the whole system, however, this shift causes a slight reduction in grass biomass rather than a sudden ecosystem shift. In other words, through the heterogeneity induced by the fire, a sudden forward shift on the level of the whole system is prevented. As more and more patches lose their grasses when herbivore density is increased, the whole system slowly becomes homogeneously tree dominated. In tree dominated patches, however, the occurrence of fire is suppressed, thereby constraining the ability of fires to create heterogeneity. In this homogeneous system, a backward ecosystem shift can be expected at the level of the whole system, rather than at the patch level.

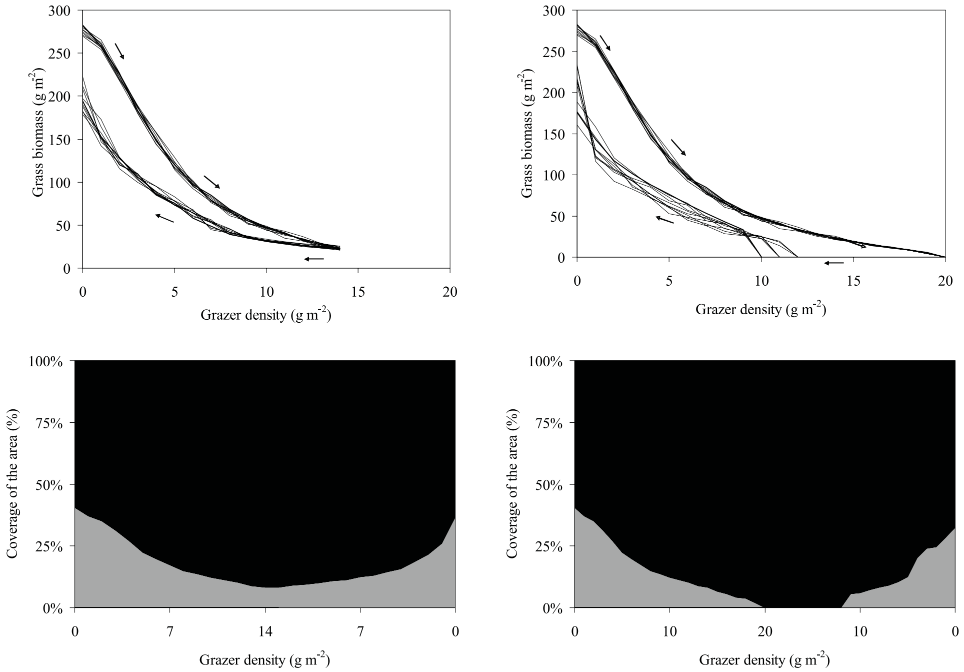


Figure 8.3 Results of two series of simulations with the spatial model that was presented in chapter 7. In the first series of simulations, grazer density was increased up to 14 g m^{-2}, and then decreased (a and c), while in the second series grazer density was increased up to 20 g m^{-2} (b and d). Figure 8.3a and b show the equilibrium grass biomass and Figure 8.3 c and d the division of tree (black) and tree-grass (grey) areas in the model for two of the simulations.

To test the above proposed mechanism, I performed some additional simulations with the model that was described in chapter 7, using parameter settings that allowed for alternative stable states, starting with low grazer densities. Grazer densities were then increased gradually. After each increase of grazer densities the amounts of grass and tree biomass were allowed to return to equilibrium before grazer density was raised to the next level. At an arbitrarily decided maximum level, I stopped increasing grazer densities, and proceeded to reduce them in a stepwise manner back to the initial low level. To avoid the extinction of grass biomass — which would yield a tree dominated system where none of the above described mechanisms can operate— I inserted a small amount of grass biomass homogeneously in the system each time grazer densities were increased or decreased. I recorded the total amount of grass biomass in the system, as well as the total cover of patches that contained grass biomass. The results of two simulations are shown in Figure 8.3.

Indeed, with progressive grazer density, the system gradually losses patches where grasses occur (Figure 8.3C and D) while the total abundance of grass biomass in the system also decreases (Figure 8.3A and B). When patches with grasses exist in the system, reversing the increasing trend of grazer densities into a decreasing one immediately leads to an increase in grass cover and abundance (Figure 8.3A and C). However, when the system becomes homogeneously tree dominated, reversing the trend does not yield an immediate response of the grass biomass (Figure 8.3B and D), despite the inserted amount of grass biomass. Only when grazer density is sufficiently reduced a sudden response of the system to decreasing grazer densities occurs: hysteresis.

Spatial processes — and the spatial heterogeneity that they can cause — can therefore reduce the probability of sudden shifts in ecosystems. When a system is spatially heterogeneous, the chances that the same event will happen everywhere is less, and therefore also the probability that sudden shifts will occur everywhere simultaneously. This behaviour of spatially heterogeneous systems has been found in other studies, and interpreted in the same way (Van Nes and Scheffer 2005). The suggestion is that sudden ecosystem shifts are more likely in systems that are homogeneous, or, that are well mixed. For example, shallow lakes are a well-studied system known to display ecosystems shifts, with a shift from a clear water state with submerged vegetation to a turbid state dominated by phytoplankton (Scheffer 1998). If the proposed hypothesis is correct, it should be no surprise that in a well mixed system such as shallow lakes, ecosystem shifts are easily recorded.

Empirical testing of this hypothesis might seem difficult, but a first step could be to analyse different empirical studies on the occurrence of ecosystem shifts and alternative stable states. In a recent review Schröder *et al.* (2005) compared a number of empirical studies that claimed to demonstrate alternative stable states. They formulated clear criteria that determine whether a system really displays alternative stables states. Studies were compared on different characteristics (*e.g.*, terrestrial vs. aquatic or field sites vs. laboratory), but not on their spatial organisation. A re-evaluation of the studies presented in their study might give a first suggestion on the realism of the proposed hypothesis.

As discussed in the introduction, a positive feedback is needed in ecosystems in order to display catastrophic behaviour. In savannas a positive feedback exists where increasing fire intensity with grass biomass induced more damage to trees which then allows greater grass production (Van Langevelde *et al*. 2003). Grazing can induce this feedback when grazing removes grass biomass, thereby reducing the fire intensity, and indirectly stimulating tree growth (Figure 8.4A). Alternatively, browsers can induce an opposite feedback, when reducing woody biomass, increases the amount of grass biomass, and through that the fire intensity (Figure 8.4). This feedback could indeed produce classical catastrophic behaviour in savannas, with sudden ecosystem shifts as a result, as shown in Figure 8.1A. In other studies where ecosystem shifts have been described, positive feedbacks also appear to be the key process to induce catastrophic behaviour. For example, in arid grazing systems, a positive feedback between vegetation presence and water infiltration could explain the local collapse of vegetation (Klausmeier 1999, HilleRisLambers *et al*. 2001). This would suggest that any system that has positive feedbacks in key processes is subject to catastrophic behaviour. In my study I found that this would be likely when systems are homogeneous, but that this is less likely in heterogeneous systems, and some shifts can even disappear (Figure 8.1). Which shift disappears depends on the system state in which the positive feedback operates (Figure 8.5). In savannas, the positive feedback mechanism applies only in patches that contain sufficient grass biomass, and not in areas that are dominated by trees and low in grass biomass. As a result, only patches that contain sufficient grass show catastrophic behaviour and sudden shifts to alternative states.

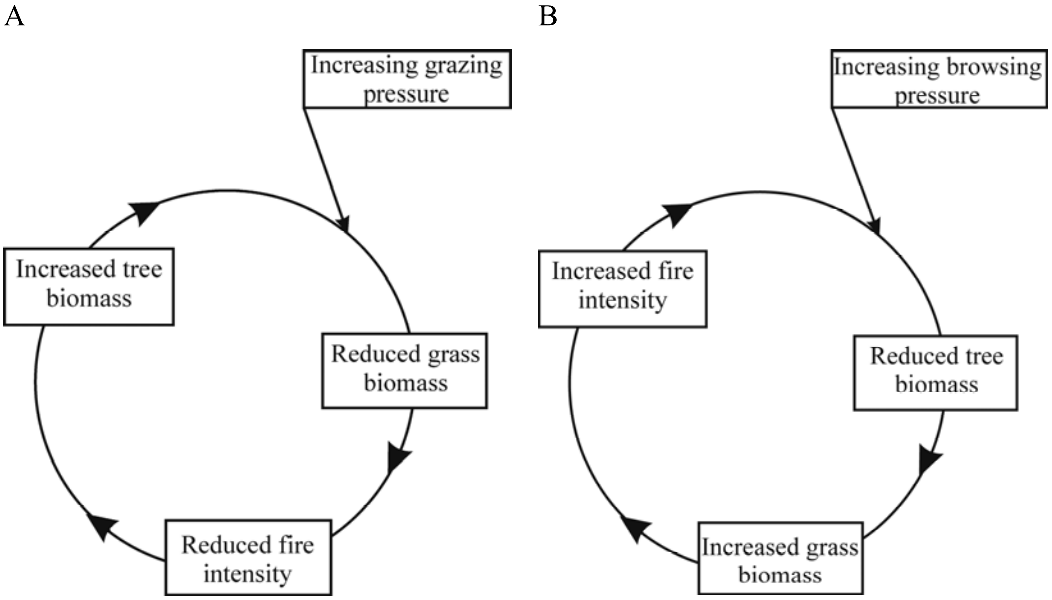


Figure 8.4 Representation of the positive feedback in savannas, and how it can be induced by grazing (A) and browsing (B).

Ecosystems that are expected to display catastrophic behaviour — because they contain positive feedbacks — and that are also spatially heterogeneous (like savannas, or arid grassland systems) could well be systems that are somewhere partway along the gradient shown in Figure 8.2. Under changing environmental conditions, the system might respond gradually to changes in environmental conditions in either direction. This might at a first glance not cause any reasons of concern. However, even though catastrophic shifts might not occur in these systems, hysteresis might still occur. When the system becomes completely homogeneous, the return to the previous heterogeneous state might not occur until conditions allow for a backward ecosystem shift (the arrow in Figure 8.2), after which the processes that create spatial heterogeneity can start operating again.

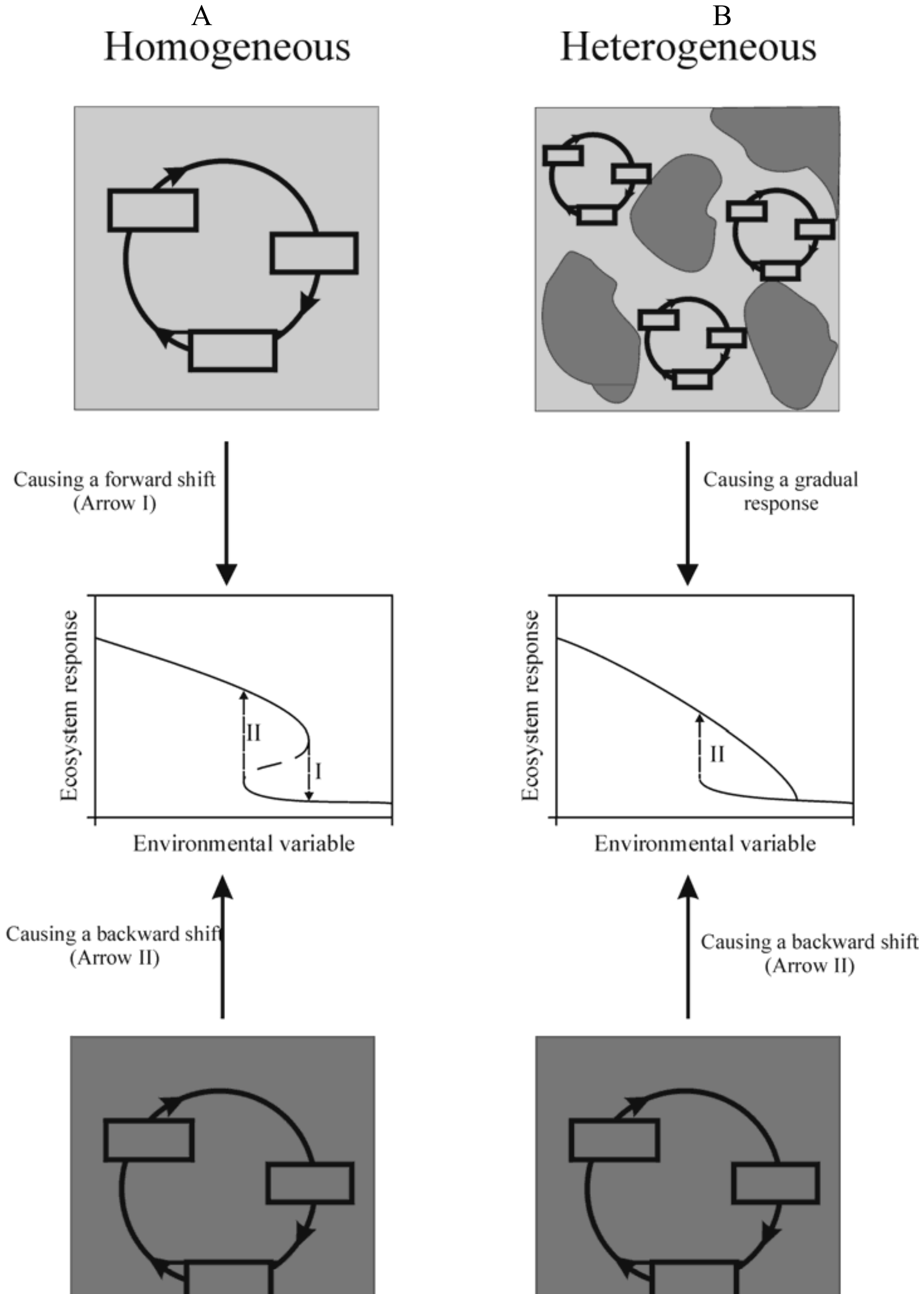


Figure 8.5 The effect of positive feedbacks in homogeneous systems (A) and heterogeneous systems (B)

Stability of encroached areas

I suggest that the heterogeneous nature of savannas prevents them from sudden shifts towards tree dominated states. Also, once the system enters the tree dominated state, this state is much more resilient, and shows hysteresis. This implies that this homogeneous tree covered state is more resilient to perturbations than the heterogeneous state in which tree and grass co-exist. However, the results on which these suggestions are based stem from models that assume that savanna systems will eventually reach an equilibrium in tree and grass standing biomass. As mentioned briefly in the introduction, some authors see savannas more as inherently unstable tree-grass mixtures (Scholes & Walker 1993, Jeltsch *et al.* 2000, Sankaran *et al.* 2004). Models based on this assumption have been able to explain tree-grass coexistence as a result of variability in driving processes in the system (Jeltsch *et al.* 1998, Higgins *et al.* 2000, Van Wijk & Rodriguez-Iturbe 2002). In an environment hostile to tree establishment — *e.g.*, dry climate or high browsing pressure — large trees can realize recruitment events only during short "windows of opportunities" — *e.g.*, during a short period of relatively wet years. If that is the case, the stability of encroached savannas, as proposed in this thesis, can be questioned. Then the time that savannas remain bush encroached depends largely on the longevity of trees. Savanna ecologists, however, have mainly focussed on the occurrence of bush encroachment events (Archer *et al.* 1988, Briggs *et al.* 2002, Brown & Carter 1998, Roques *et al.* 2001, Van Auken 2000, Prins & Van der Jeugd 1993) rather than the retreat of trees (Dublin *et al.* 1990, Van de Vijver *et al.* 1999). Thorough investigation of the stability of bush encroached areas is a feature of savanna ecology that, so far, has been relatively unexplored.

A useful first step would be to formulate a simple model that incorporates the longevity of large trees, and takes account size effects, as these are important determinants of the longevity of trees. Large trees are less susceptible to browsing (Van de Koppel & Prins 1998, Goheen *et al.* 2007) and fire (De Ronde *et al.* 2004), and are able to produce recruitment events. As shown in fish population models, size-dependent life-history traits can promote catastrophic shifts in fish population densities (De Roos & Persson 2002). Two general characteristics are required for this kind of ecosystem behaviour. First, individual growth is positively correlated with individual size and with the amount of resources obtained through the root system. Second, individual mortality decreases with body size. These characteristics are very much representative for savanna tree species. Seedling establishment is seriously hampered by the presence of larger trees or dense grass swards (Loth *et al.* 2005). Also small trees are damaged more by fire than large ones (De Ronde *et al.* 2004) and seedlings compete for water with grasses, increasing their mortality.

Insights from a modelling study incorporating the life history traits of trees should yield testable hypotheses that predict when bush encroached areas are stable, and when they are a temporal state that will disappear as tree mortality and reduced regeneration lead to more grass cover resulting in a return to a savanna state. This would help in formulating proper field experiments to investigate the stability of encroached areas.

Implications for savanna management

These results have implications for the management of savanna ecosystems. Many studies have addressed the sudden shift of savannas from tree-grass co-occurrence to ones dominated by trees (Archer *et al.* 1988, Briggs *et al.* 2002, Brown & Carter 1998, Roques *et al.* 2001, Van Auken 2000). These shifts are often attributed to several factors. Changes in tree dominance in savannas are attributed to overgrazing by livestock and changes in the fire regime in combination with occurring droughts (Walker *et al.* 1981, Scholes & Walker 1993, Roques *et al.* 2001). A loss of heterogeneity might have contributed to these shifts as well (chapter 7). In chapter 5 I found that with high levels of herbivory, spatial heterogeneity (both in terms of the size of the patterns, as well as the overall variability) can be reduced, and that maximal spatial heterogeneity is maintained at intermediate herbivore levels. The homogeneous state that is created by high grazing pressure is also a state that does not allow for an important spatial process (fire) to generate heterogeneity because the amount of fuel in the system is reduced. This suppresses the buffering mechanism described in chapter 7, resulting in an increased probability of a system wide shift increases.

Another well know example where a sudden increase in cover of woody species occurred, was during the rinderpest pandemic at the end of the 19th century in East Africa. This pandemic eradicated large numbers of wildlife and livestock populations and caused famine and starvation in the human population. This reduced the occurrence of anthropogenic fires (which constitute most of the savanna fires, Pyne *et al.* 2004) and herbivory (Dublin *et al.* 1990, Prins & Van der Jeugd 1993, Prins 1996). As shown in chapter 4, a decrease in herbivory can also result in a reduction of spatial heterogeneity, and chapter 7 showed that reducing the occurrence of fire increased the establishment and growth of woody species. The combined effects of loss of spatial heterogeneity and the increased growth of woody species could be responsible for the observed shift. In subsequent years, the human population recovered, and with that, the occurrence of anthropogenic fires and herbivore numbers, which was associated with a decline of woody biomass (Sinclair 1979). This suggests that spatial heterogeneity in savannas increases the stability of the system, making a sudden shift from one state to the other less likely. Consequently, maintaining a heterogeneous system could be a preferred objective, depending on the management goals. Herbivory and fire can induce and maintain this heterogeneity (chapters 3-5), and may prove to be useful tools for managers to increase the heterogeneity of the area under their responsibility. However, increasing spatial heterogeneity also leads to lower equilibrium grass biomass (chapter 7), which—from the perspective of cattle ranching— can conflict with the management objective (Tobler *et al.* 2003, Sharp & Wittaker 2003). Therefore, it could well be that from an economic point of view a homogeneous state is still the preferred state, despite the higher risk of sudden shifts. In this case managers have to be careful not to come close to a point where catastrophic shifts can occur. As shown in chapter 6, an adaptive scheme in which herbivores are removed quickly when the vegetation starts to degenerate, and animals are only returned after the vegetation is recovered completely can increase the stability of the system. This again would not be an optimal solution for managers that want to maximize cattle production, because cautious removal of cattle before severe degradation might not utilize the complete production potential on the short term. However, on the long term this could prove the better choice as continuation of production can be assured.

Conclusion

In this thesis I investigated the effects of spatial processes and patterns on savanna system stability. I found that both herbivory and fire can cause spatial heterogeneity under specific conditions (chapters 3, 4 & 5). I also found that including spatial heterogeneity in model analyses of savannas suggest that the savanna system becomes less prone to ecosystem shifts. I concluded that heterogeneity is the main factor reducing this sensitivity of savannas to ecosystem shifts. However, although the system might be less susceptible to ecosystem shifts, once it becomes tree dominated, results suggest that it will remain tree dominated. I end by suggesting that the stability of areas encroached by woody species should be further investigated to test this heterogeneity hypothesis.

Summary

Introduction

Savannas cover around 12% of the global landmass and are of economic importance for about 20% of the world population that lives in these areas. The ecosystem services that savannas provide for this part of the human population includes livestock and fuel wood production and wildlife conservation, which in its turn can generate income through tourism. In order to maintain the quality of these services, an understanding of the functioning of this ecosystem is necessary. Especially detailed knowledge on how the system responds to key determining factors like fire and herbivory is crucial, as these are factors that can be managed.

An important feature in the savanna ecosystem is that it is able to show sudden shifts from one stable state, with both trees and grasses present, to another stable state with only trees, *i.e.*, bush encroachment. A functional understanding of how processes like herbivory and fire can induce or reduce these shifts helps in the formulation of proper management strategies for these ecosystems and to maintain the quality of its services.

An emerging issue in ecology that is relevant with respect to the occurrence of ecosystem shifts is the effect that spatial patterns and processes can have on ecosystem dynamics. Spatial processes are hypothesised to mediate the occurrence of ecosystem shifts and increase the stability of ecosystems.
Three questions were leading:
1-"What is the effect of spatial heterogeneity on spatial processes"
2-"How is spatial heterogeneity created by spatial processes?" and
3-"Is the occurrence of sudden ecosystem shifts influenced by these spatial patterns and processes?"

Origins of patterns

To explore the first two leading questions we investigated the correlations between spatial patterns and possible explaining variables in Chapter 2. Because trees and grasses are contrasting on aerial photographs, we focussed on tree patterns in savannas. We found that bottom-up factors — that are not under control of humans — might set important boundaries to what tree patterns are possible, but that top-down factors — that can often be controlled by humans — correlate better with tree patterns. Within boundaries — set by abiotic factors — we found that fire frequency — which can to a certain extent be controlled by humans — and the density of the human population itself, are important factors explaining the variation in nearest neighbour distances. Next to fire, herbivory can also be a potential source of spatial pattern in savannas, and we found an effect of sheep and goats on the variation in patch sizes of trees.

Fire

The correlation between fire frequency and variation in nearest neighbour distances between trees suggests that by protecting each other against the destructive effect of fires, trees close to each other facilitate one another. More specifically, high fire frequencies should then induce a clustered organisation of trees. In chapter 3, we investigated this, making use of a burning experiment that was initiated in 1958 in the Kruger National Park, South Africa. The analysis showed that fire frequency can

increase the clustering of same species clusters in areas that have a high clay content in the soil. Also we found that, although fire frequency influences the clustering of trees, limited dispersion of seeds of trees is more important in determining clustering of savanna trees. This suggests that the clustered organisation of trees often found in savannas is a function of the number of juvenile trees present near mother trees, their competitive interaction for water in the upper soil — positively influenced by the amount of clay in the soil — and the frequency with which these saplings are burned. We also found that once trees are in close vicinity of each other, they do mitigate the damage that fires can inflict on them.

How trees can protect each other against the destructive effects of fire depends on the spatial arrangement of these trees (*i.e.*, clustered or not), but also on the effect these trees have on fires. We know that many tree and bush clusters in savannas are capable of suppressing the amount of grass under their canopy, which is the main fuel for savanna fires. Therefore it can be difficult for a fire to penetrate a cluster. Also, clusters can reduce wind speed, creating a different micro climate at the leeward side of a cluster compared to the windward side. It could be expected that, when a fire hits a dense tree cluster, the trees on the windward side are more damaged by the fire, than trees on the leeward side. We tested this in an experimental set up with artificial bush clusters as described in box 3.1. We found the opposite effect of clusters and their size on the impact of fires than expected. Two possible explanations can be given. First, it is possible that the microclimatic conditions at the leeward side of clusters are differently modified than expected. Secondly, it could also be that the artificial clusters are not mimicking real life tree and bush clusters correctly. Therefore a new experiment should be organised in which fire behaviour around differently sized bush clusters will be investigated.

Herbivores

In chapter 2 we found that herbivores have a negative effect on the variation in patch sizes of trees. Also we found in our analyses of tree clustering (chapter 3) that herbivory might have potential consequences for the spatial arrangement of trees. In order to explore these relations further, we performed two modelling studies, where we analysed the interactions between herbivory and tree patterns in savannas.

In the first modelling study, we analysed the effects of spatially explicit foraging in a spatially explicit model (chapter 4), including both trees and grasses as plant components. We included grazers and browsers, and assumed constant herbivore densities. Also we assumed complete knowledge of the environment for herbivores, and included “ self facilitation” and “spatially explicit foraging” as processes that might explain patterning in the vegetation by herbivores. Self facilitation means that foraging can increase the quality or quantity of forage in a patch. Spatially explicit foraging means (i) that herbivores select patches to forage based on the average quality of that patch and surrounding patches, and (ii) that once foraging in a selected patch they also forage a minor amount in surrounding patches. We found that both self facilitation and spatially explicit foraging were needed for herbivores to create spatial patterns in the vegetation. More specifically, at intermediate foraging levels, the interaction between spatially explicit foraging and self facilitation increased the size of foraging patches as well as the over all variation in the system.

In a second modelling study, we relaxed the assumption of constant herbivore pressure. We used a simple and analytically tractable reaction-diffusion approach. We assumed that trees and grasses compete for water, and disperse slowly to neighbouring locations, which was simulated as a diffusion process with low diffusion coefficients. Available plant biomass was assumed to promote herbivore pressure. Herbivore pressure was assumed to redistribute fast in space, and was therefore simulated as a diffusion process with high diffusion coefficients. The result of these assumptions was that we obtain a system in which herbivore pressure at a given location is not only a function of the amount of available forage at that location, but also of available forage at surrounding locations: spatially dependent foraging. We showed that this system is able to produce spatially non-homogeneous patterns. This suggests that when herbivores are not kept at constant densities, only spatially explicit foraging by itself can already create patterns in savannas.

Effects of spatial processes

Apart from the interactive effects of spatial patterns and processes, we wanted to investigate the effect of these patterns and processes on the stability of savannas. More specifically, we were interested in the possibility of the occurrence of sudden ecosystem shift when spatial patterns occur. In savannas sometimes a sudden shift from a tree-grass co-dominance to a state of only tree dominance — so called bush encroachment — is observed. Related to the occurrence of ecosystem shifts is the stability of ecosystems, which can be defined as the amount of perturbation the system can absorb without shifting to a different stable state. In the previous chapters we found that both savanna fires and herbivory can play an important role in the spatial patterns in the savanna ecosystem. We investigated both the effect of the spreading of fires as well as the effect of dynamically responding herbivores on ecosystem stability and the occurrence of ecosystem shifts.

We started investigating the interactive effects of herbivores responding to vegetation dynamics on savanna behaviour. We modelled the interaction between dynamics of both browsers and grazers, and trees and grasses respectively with a simple non-spatial model (chapter 6). The model showed that including negative feedbacks between herbivores and plants into the model decreased the chances for ecosystem shifts to occur. Important parameters that regulated the occurrence of these shifts were the rates with which herbivores respond to changes in forage availability. Especially the growth rate and mortality rate of herbivores were important. With low mortality and high growth rates we found that alternative stable states occurred under wide ranges of parameters, but this occurrence was reduced when increasing the mortality — *i.e.*, herbivores show a fast decline when less forage is available — or when decreasing the growth rate — *i.e.*, herbivores respond slowly when more forage becomes available.

In chapter 7, we analysed the effect that spatially explicit burning has on the occurrence of ecosystem shifts and the stability of the savanna ecosystem. We formulated a spatially explicit model that contained grasses, trees, grazers and browsers. We included fire as a spatial process, where savanna fires were modelled spreading from randomly located ignition points. The spreading of fire was assumed to be a function of the amount of grass biomass present in locations that the fire was spreading towards. We varied the scale of fires, by varying the time that fires could spread through the simulated landscape. We also performed simulations, where fires were not spreading through the landscape. Here fires were applied as a blanket — each location was forced to burn, irrespective of the amount of grass biomass present. We found that simulating fire as a spatial process increased the range of environmental conditions where ecosystem shifts can occur. However, when taking a closer look at the exact dynamics in the system, we learned that a sudden shift from

tree-grass co-dominance to only tree dominance disappears. In other words, the risk of bush encroachment was less when fires were modelled spatially explicitly.

In the synthesis (chapter 8) I showed the relation between the different chapters, and elaborated on the finding of chapter 7. I attributed the loss of a sudden bush encroachment to the heterogeneity in the system. I performed additional analyses with the model formulated in chapter 7 and found that, although indeed the risk of a sudden bush encroachment event disappears, hysteresis still occurs. Once the system is completely covered by trees the system will not easily return to a tree-grass co-dominance. I raised the suggestion that the stability of bush encroached areas should be further investigated in order to test this finding.

Conclusion

This thesis shows that fire and herbivory are capable of creating and maintaining spatial heterogeneity. Also, it showed that the negative effect of fire on trees is reduced when trees are organized in clusters. Finally it was found that spatially heterogeneous systems are less prone to sudden ecosystem shifts than homogeneous systems. However, once a savanna becomes completely tree dominated, it will not easily return to a tree grass savanna.

Samenvatting

Inleiding

Savannes zijn ecosystemen met een continue grasbedekking en een discontinue boombedekking. Wereldwijd bedekt dit ecosysteem ongeveer 12% van het landoppervlak. Savannes zijn een belangrijke bron van inkomsten voor 20% van de wereldbevolking, ondermeer door extensieve veehouderij, productie van brandhout en toerisme. Om de benutting van dit ecosysteem te kunnen garanderen is een functioneel begrip van savannes onontbeerlijk.

Een belangrijk fenomeen dat wordt waargenomen in savannes is de plotselinge ecosysteemverschuiving, naar een systeem met een continue boombedekking (verbossing). Een gedegen begrip van de invloed van processen zoals herbivorie en vuur op deze verschuivingen is van belang om goede beheersstrategieën voor savannes te kunnen opstellen.

Het belang van ruimtelijke processen krijgt steeds meer aandacht binnen de ecologie. Ruimtelijke processen kunnen mogelijk een rol spelen in de dynamiek van ecosysteemverschuivingen. Mijn hypothese is dat ruimtelijke dynamiek ecosysteemverschuivingen kan verhinderen en de stabiliteit van een ecosysteem kan vergroten. Dit is onderzocht aan de hand van de volgende drie hoofdvragen:
1-"Wat is het effect van ruimtelijke heterogeniteit op ruimtelijke processen?"
2-"Hoe wordt ruimtelijke heterogeniteit gevormd door ruimtelijke processen?" en
3-"Worden plotselinge ecosysteemverschuivingen beïnvloed door ruimtelijke processen en patronen?"

Ontstaan van patronen

Om de eerste twee hoofdvragen te beantwoorden, is de correlatie tussen ruimtelijke patronen en mogelijk verklarende factoren onderzocht (hoofdstuk 2). De ruimtelijke patronen van bomen in savannes zijn goed te onderscheiden op luchtfoto's en zijn daarom voor deze analyse gebruikt. De resultaten wijzen uit dat factoren die planten bovengronds beïnvloeden (zoals herbivoren of vuur) correleren met boompatronen. Vuurfrequentie correleert met de afstand tussen bomen, en de aanwezigheid van schapen en geiten correleert met de variatie in de grootte van boomgroepen. De correlaties met factoren die de boomgroei reguleren zijn minder sterk. Deze regulerende factoren stellen waarschijnlijk grenzen aan patroonvorming, zoals de maximale boombedekking of de grootte van boomgroepen.

Vuur

De correlatie tussen vuurfrequentie en de afstanden tussen bomen suggereert dat bomen elkaar kunnen beschermen tegen de negatieve effecten van vuur in savannes. Dit wijst op facilitatie tussen bomen. Hoge vuurfrequenties zouden dan moeten leiden tot een groepering van bomen in de ruimte. Dit is onderzocht in hoofdstuk 3, door de groepering van bomen in kaart te brengen in het Kruger Park in Zuid-Afrika. Hier wordt al sinds 1958 een brandexperiment uitgevoerd.

De analyses laten zien dat hoge vuurfrequenties de groepering van bomen van dezelfde soort op kleigronden kunnen verklaren. Daarnaast blijkt de beperkte verspreiding van jonge boompjes rondom de moederboom een belangrijke factor. Dit suggereert dat de groepering van bomen een gevolg is van het aantal jonge bomen rondom de moederboom, de ondergrondse concurrentie om water tussen de jonge bomen en de moederboom (welke wordt beïnvloed door het kleigehalte in de bodem) en de vuurfrequentie. We vonden ook aanwijzingen dat bomen die dicht op elkaar staan minder negatieve effecten van vuur ondervinden.

Hoe bomen elkaar kunnen beschermen tegen de negatieve effecten van vuur hangt af van de ruimtelijke verspreiding van bomen (mate van groepering), maar ook van het effect dat deze bomen hebben op vuur. Gras is de belangrijkste brandstof voor savannebranden. Boomgroepen in savannes zijn in staat om de hoeveelheid gras onder hun boomkroon te reduceren. Dit belemmert de voortgang van savannebranden in en rond boomgroepen. Boomgroepen beïnvloeden ook de lokale windsnelheid, waardoor het microklimaat kan verschillen tussen de leizijde en de loefzijde. Daarom verwachtten we een ernstigere brandschade aan de loefzijde dan aan de leizijde. Dit is getoetst in een experiment waarbij we gebruik maakten van kunstmatige boomgroepen (Box 3.1). Hieruit blijkt een tegenovergesteld effect. De kunstmatige boomgroepen wakkerden de intensiteit van branden aan. Hier geven we twee verklaringen voor. Ten eerste is het mogelijk dat boomgroepen het microklimaat aan de leizijde anders beïnvloedden dan verwacht. Ten tweede kan het zo zijn dat de kunstmatige boomgroepen de werkelijkheid niet goed benaderen. Om dit verder te onderzoeken is een vervolg op dit experiment met natuurlijke boomgroepen nodig.

Herbivoren

Uit de bevindingen van hoofdstuk 2 blijkt dat er een correlatie bestaat tussen herbivoren en de grootte van bomen. Onderzoek beschreven in hoofdstuk 3 wijst ook uit dat herbivoren een rol kunnen spelen bij de vorming van boomgroepen. Om het effect van herbivoren op boompatronen verder te onderzoeken hebben we twee modelstudies uitgevoerd (hoofdstuk 4 en 5).

In de eerste studie (hoofdstuk 4) hebben we de effecten van ruimtelijk foerageren onderzocht in een simulatiemodel. Voor de vegetatiecomponent werden bomen en grassen gemodelleerd. Grazers en bladeters werden als aparte herbivoorgroepen meegenomen, hierbij werd aangenomen dat de herbivoordichtheid gelijk bleef. Bovendien gingen we ervan uit dat de herbivoren complete kennis hadden over de verspreiding van bomen en grassen door het gebied. “Zelffacilitatie” en “ruimtelijk foerageergedrag” werden als mogelijk verklarende processen voor ruimtelijke patronen in de modelsimulaties meegenomen. Zelffacilitatie betekent in dit geval dat een herbivoor door zijn foerageergedrag de kwaliteit of kwantiteit van zijn voedsel kan verbeteren. Ruimtelijk foerageergedrag betekent dat herbivoren een foerageerplek kiezen op basis van de gemiddelde voedselkwaliteit en -aanbod van de desbetreffende plek en de daaraan grenzende plekken. Hierbij wordt verondersteld dat wanneer ze foerageren in een uitgekozen plek, ze ook een kleine hoeveelheid voedsel wegnemen in de aangrenzende plekken. De resultaten lieten zien dat beide mechanismen nodig zijn om ruimtelijke patronen door herbivorie te laten ontstaan.

In de tweede studie (hoofdstuk 5) maakten we gebruik van een simpel analytisch traceerbaar reactie-diffusiemodel. Hierbij is de aanname van een constante herbivoordichtheid losgelaten, omdat deze niet realistisch werd geacht voor natuurlijke systemen. Wel namen we aan dat bomen en grassen concurreren om water en dat ze langzaam dispergeren naar aangrenzende locaties. Dit laatste kan worden nagebootst door een diffusieproces met langzame diffusiesnelheden. Ook namen we aan dat de herbivorendruk zich snel verdeeld over het landschap. Dit werd nagebootst door een diffusieproces met hoge diffusiesnelheden. In het model wordt lokale herbivorendruk gereguleerd door de aanwezige plantenbiomassa. Het resultaat van deze aannames is dat lokale herbivorendruk niet alleen een gevolg is van de plantenbiomassa ter plekke, maar ook van de plantenbiomassa in de omgeving: ruimtelijk foerageergedrag. De modelresultaten laten zien dat ook dit systeem in staat is om ruimtelijke patronen te genereren. Dit suggereert dat wanneer herbivoren niet op constante dichtheden worden gehouden, zelffacilitatie niet nodig is om vegetatiepatronen door herbivorie te laten ontstaan. Alleen ruimtelijk foerageergedrag kan dan al leiden tot vegetatiepatronen.

Effecten van ruimtelijke processen

In savannes komen soms plotselinge ecosysteemverschuivingen voor van boom-gras-co-existentie naar boomdominantie, zogenoemde verbossing. Om meer inzicht te kunnen krijgen in de processen achter deze verschuivingen, wilden we weten wat het effect van ruimtelijke patronen en processen is op deze plotselinge ecosysteemverschuivingen. Gerelateerd aan deze plotselinge ecosysteemverschuivingen is de stabiliteit van een ecosysteem. Deze kan worden gezien als de hoeveelheid verstoring dat een systeem kan verdragen zonder te verschuiven. In de vorige hoofdstukken vonden we dat vuur en begrazing een rol kunnen spelen in de formatie en instandhouding van ruimtelijke patronen in savannes. Daarom hebben we verder onderzocht wat het effect is van het ruimtelijk verspreiden van vuur en het dynamisch reageren van herbivoren op de stabiliteit van savannes.

We begonnen door de interactie tussen het aantal herbivoren en plantenbiomassa te modelleren (hoofdstuk 6). Dit model liet zien dat de kans op plotselinge ecosysteemverschuivingen verminderde als plantenbiomassa herbivorenaantallen reguleert. Belangrijke parameters die deze kans beïnvloeden zijn de groeisnelheid en de mortaliteit van herbivorenpopulaties. Met lage mortaliteit of hoge groeisnelheden vinden ecosysteemverschuivingen vaker plaats.

Het effect dat de ruimtelijke verspreiding van vuur heeft op de stabiliteit van savannes is bestudeerd in hoofdstuk 7. Hiervoor creëerden we een ruimtelijk expliciet simulatiemodel met daarin bomen, grassen, grazers en bladeters. Vuur was gemodelleerd als een ruimtelijk proces, waarbij het zich verspreidde vanuit willekeurig aangestoken plaatsen. Er werd aangenomen dat de verspreiding van vuur een functie is van de hoeveelheid beschikbaar gras op plekken waar het vuur naartoe beweegt.

Een belangrijke stuurvariabele in dit model was de grootte van de branden. Deze werd gevarieerd en gecontroleerd door de tijd aan te passen die het vuur kreeg om zich door het landschap te verspreiden voor het uitdoofde. Als controle werden er ook simulaties uitgevoerd waarbij vuur niet ruimtelijk werd gemodelleerd. Hierbij werd elke plek aangestoken, onafhankelijk van de hoeveelheid aanwezig gras. De resultaten lieten zien dat wanneer vuur zich als een ruimtelijk proces door savannes verspreidt, de kans op een systeem dat zowel boom dominantie als boom-gras-co-existentie toestaat (twee alternatief stabiele toestanden) toeneemt. Dit suggereert dat de kans op plotselinge ecosysteemverschuivingen toeneemt. Echter, een nadere analyse liet zien dat alleen plotselinge verschuivingen van boomgedomineerde systemen naar boom-gras-co-existentie voorkwamen, maar dat omgekeerde verschuivingen verdwenen. In andere woorden, het risico op verbossing nam juist af als vuur ruimtelijk expliciet was gemodelleerd.

De synthese (hoofdstuk 8) toont de relatie aan tussen de verschillende hoofdstukken en gaat verder in op de bevindingen van hoofdstuk 7. Het verdwijnen van plotselinge verschuivingen van boom-gras-co-existentie naar een door bomen gedomineerd systeem werd in dit hoofdstuk door mij verklaard door het feit dat savannes hun ruimtelijke heterogeniteit verliezen als ze langzaam maar zeker dichtgroeien met bomen. Om dit te verifiëren werden extra simulaties uitgevoerd. Deze lieten zien dat plotselinge verschuivingen inderdaad verdwenen, maar dat wanneer het systeem door bomen wordt gedomineerd, het niet snel zal terugveranderen in een boom-gras-co-existentie. Dit wordt hysterese genoemd. In dit hoofdstuk suggereer ik dat de stabiliteit van verboste savannes verder onderzocht moet worden om de validiteit van dit modelresultaat te onderbouwen.

Conclusie

Dit proefschrift laat zien dat vuur en herbivorie in staat zijn om ruimtelijke patronen te creëren en in stand te houden. Bovendien laat het zien dat het negatieve effect van vuur op bomen minder wordt als bomen in groepen in de ruimte zijn georganiseerd. Ruimtelijk heterogene ecosystemen blijken minder gevoelig te zijn voor plotselinge verschuivingen, dan homogene gebieden. Echter, zodra een savanne eenmaal geheel verbost is, zal het niet gemakkelijk terugkeren naar zijn oorspronkelijke staat.

Acknowledgements

As most theses go, only few get the credits for the hard work that has been done, while many have contributed. That is not any different with this thesis. Although some of the hard working people have been acknowledged in some way by means of a co-authorship or by being mentioned in the acknowledgement section of a chapter, many remain unmentioned. I hope to be able to mitigate this unfair situation in this section of my thesis. Of course I will try to be as complete as possible, but whoever feels unrightfully left out can always get in touch with me, and then we'll settle things over a beer.

It's difficult to decide where to start, but it feels right to begin with the people who initiated the whole process that started off this thesis, Frank van Langevelde and Claudius van de Vijver, by writing the proposal. They were always at my side when needed to advise me and support me. To me, in retrospect the whole process feels like a smooth drive, and much of that is to your credit. Thanks for the great time together, and the unwavering believe in my capacities, which was sometimes lacking by myself.

Also my promotor, Professor Herbert Prins attributed greatly to the progression of this thesis. I still remember the first time we officially shook hands in the Dorges' Hotel in Kibber, North India, and got to learn each other better over cheap Indian whisky and tax free Dutch cigars. Since then, I learned many things from you on how science should be performed and applied. But most of all, I learned from you that science should be fun, which it definitely was for the last four years.

Somebody with whom I "involuntarily" spent a lot of time in these last four years was my room mate Geerten Hengeveld. Geerten we started together and plan to finish the job together as well. Thanks for the many inspiring chats during our hours in the office, as well as the activities besides the work. I feel very lucky ending up with you in one room, and hope that ending both our theses does not mean ending staying in touch.

In this thesis many MSc. Students participated, of which three projects yielded a chapter, and one project resulted in an extra Box included in this thesis. Thanks for your dedication and hard work Henjo, Bob, Laura, Dieter and Anneloes.

Working at the Resource Ecology Group was fun! The main reason was that all the colleagues in the building were great to work with, lunch with, have "borrels" with, drink coffee with or canoe with. Therefore, in random order (yes I randomized it in Excel) Xavier, Roy, Gerda, Nicol, Jelle, Jort, Daan, Toos, Marleen, Edward, Jessica, Brian, Willemien, Herman, Fred, Ignas, Jan (B.), Geert, Tom (vd H.), Frans, Elmar, Maurits, Anne-Marie, Jasper (vd L.), Anil, Margreet, Herbert, Flavia, Christiaan, Tom (H.), Petra, Miriam, Juul, Pim, Arina, Jinze, Eduardo, Geerten, Bjorn, Monique, Beatrijs, Jan (v W.),Louis, Frank (B.), Jasper (v R.), Rudy, Maureen, Jasja, Henjo, Tsewang, Mariaan, Ivonne, Gabriela, Joost, Dick, Tony, Wim, Yolanda, Angela, Veronique, Frank (v L.), Milena, Emanuel, Sip, Cornelis, Robert, Christine, Farshid, Andre, Ralf, Karle, Ania, Audri, Eelke, Steven, Arend, Barend, Euridice, Jelle, Michael, thanks for the great time!

During the course of this project I was allowed to visit South Africa twice, and both times were a great experience. This was only possible because of the support of many people in South Africa. Although I fear that the following list will be far from complete, I would like to pay a special thanks to Winston and Lynne Trolloppe, William Bond, Navashni Govender, Glynn Allard, Louise Rademan, Johane Baloy, Tembi (Steven), Rina Grant, Harry Biggs, Mariska, Joris, Dieter, Claudius, Frank,

Coby, Dumi, Wellington, Mweli, Matthew, Fiona, Toby, Stef, and the complete Johannesburg crew! Thanks so much for provided assistance, hospitality, and companionship during the many sundowners and braai's, and I hope to meet you all more often in the future.

Although South Africa seems far, Enschede may seem even further when taking the public transport from Wageningen. I had the pleasure of meeting many PhD students and staff members of the ITC, and it was always great teaming up with them. I especially want to thank Jan de Leeuw for his support and suggestions while working with aerial photographs from the ITC archive. Jan, I'm looking forward to team up with you and your colleagues more often in the future.

Besides working as a scientist, I was also offered the opportunity to work in the PhD Student Platform (PSP) of the graduate school, where I learned a lot about the politics behind science. Being a member of the PSP has been an inspiring experience, and I want to thank Evert, Daniel, Erik, Stefan (d G.), Santiago, Agniezka, Jeroen, Arnaud, Andre, Bas, Stefan (B.), Marjolijn, Ale, Henjo, Edwin, Mark, Diego, Jochem and Claudius for making the PSP fun.

A special word of gratitude should be directed to John Ludwig and Peter Frost for voluntarily reviewing my synthesis chapter. With sufficient distance to my work, but with indepth knowledge on savanna's they offered valuable comments that helped me improve the synthesis.

Because modeling doesn't require much physical exercise it can lead to an excessive build-up of surplus energy. Luckily there was a reliable group of people that was willing to provide the necessary conditions to get rid of aggression on a squash ball. Gert-Jan, Mart-Jan, Hugh, Geerten, Ronald and Detmer, thanks for that. Also outside office hours many people helped to stay focused and to continue. A great past-time activity has been playing Jazz music together with Jasja and Chris. Thanks for bringing back playing saxophone in my curriculum!

De Clique has been a continuous inspiration for this thesis, someone has to be the first! But I'm confident that more Cliquo's will follow on the path of a PhD. Hetty, Stef, Mechteld, Marieke, Leontien, Ulrik, Bram, Peter and Michelle, thanks for continuous friendship, useless borrel discussions and past and future Clique activities.

Although squash has been a useful way of getting rid of surplus energy, more physical and mental distraction was provided by Jiu-Jitsu. Martijn and Judith, thanks for accepting my limited motoric capacity and the resultant physical injury without a complaint or retaliation. Also the shared interest for cigars has been crucial for this PhD.

Many other friends have been involved in one or more way's for out of office occupation, and I want to thank you all for your friendship, Suus, Sander, Janette, Peter, Manon, David, Bastiaan, Yme, Robert, Theo, Gert-Jan, Nynke, Wouter, Jasper, Stefan, Sanne, Karsten, Nienke, Michel, Jaqueline, Sander, Yvonne, Trevor and many others.

My family has been very important in many ways, Heit, Mem, Luc, Ady, Marijke, Nynke, Rob, Reinou, Elske, Frank and Jesper, thanks for being there! Finally, and certainly the most important person to thank is my wonderful wife, for continuous support and everlasting back-up. Michelle, I love you.

Affiliations of authors

Anneloes L. de Raad
Evolutionary Anthropology Research Group, Department of Anthropology, University of Durham, 43 Old Elvet, Durham DH1 3HN, UK

Claudius A.D.M. van de Vijver
Plant Production Systems Group, Wageningen University, PO Box 430, 6700 AK Wageningen, The Netherlands

Frank van Langevelde
Resource Ecology Group, Wageningen University, PO Box 47, 6700 AA Wageningen, The Netherlands

Henrik J. de Knegt
Resource Ecology Group, Wageningen University, PO Box 47, 6700 AA, Wageningen, The Netherlands

Herbert H.H.T. Prins
Resource Ecology Group, Wageningen University, PO Box 47, 6700 AA, Wageningen, The Netherlands

Jacob C. Douma
Department of Systems Ecology, Vrije Universiteit Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

Jan de Leeuw
International Institute for Geo-Information Science and Earth Observation, P.O. Box 6 7500 AA Enschede, The Netherlands

Navashni Govender
South African National Parks, Scientific Services, Private Bag X402, Skukuza, 1350, Republic of South Africa

Curriculum Vitae

Thomas Anne Groen was born on 5 September 1978 in Friesche Palen, the Netherlands. He obtained his high school degree in 1996 at the CSG Dingstede in Meppel. After that he started with the MSc. Tropical Land Use at Wageningen Univerity. During his MSc he stayed for a period of four months in India for an internship in the Trans Himalayas, where he paryicipated in a vegetation survey. After that he performed a study on how to model the competition for water between trees at ALTERRA for the spatially explicit forest ecosystem model FORSPACE. Here he obtained his first modeling experience. Then he visited the Tropical Forest Research Centre of the CSIRO in Australia for nine months as a part of his thesis work. Here he investigated the connectivity of rainforest fragments. This provided hem with usefull experience in GIS applications and remote sensing.

He graduated at the end of 2001 and was appointed in 2003 at ALTERRA as a junior researcher in a project dealing with the calculation of CO_2 sequestration in forests. For this project he developed and implemented a cost accounting module in an existing sequestration modeling tool called CO2Fix. This offered the opportunity to learn the first principles of C++ programming, as well as it introduced him to the complex international climate negotiations under the Kyoto protocol of the UNFCCC.

Beginning 2003 he started his PhD project at the Resource Ecology Group of prof. Herbert Prins at Wageningen University, of which this thesis is the end result. During this research he visited South Africa twice for field work, but spent most of his time on modeling savanna dynamics in the office.

At the moment he is appointed as researcher at ALTERRA in an EU-funded project dealing with the adaptation and mitigation options for the European Union, with special reference to forests.

List of publications

In international Journals

Groen, T.A., Nabuurs, G.J., and Schelhaas, M.J. 2006. Carbon accounting and Cost estimation in forestry projects using co2fix v.3. *Climatic Change* **74**: 269-288.

Kramer, K., Groen, T.A. and Van Wieren, S.E. 2003. The interacting effects of ungulates and fire on forest dynamics: an analysis using the model FORSPACE. *Forest Ecology and Management* **181:** 205-222.

Submitted and in preparation

Hengeveld, G.H., Van Langevelde, F., Groen, T.A. & De Knegt, H.J. (in prep) Optimal foraging for multiple resources in several food species.

Groen, T.A., Van Langevelde, F. & Van de Vijver, C.A.D.M. (in prep) The spatial scale of fire influences the stability of savanna ecosystems.

Douma, J.C., Van Langevelde, F., Groen, T.A., Van de Vijver, C.A.D.M. & Prins, H.H.T. (in prep) Spatial patterns in savanna trees and grasses due to herbivory.

Groen, T.A., Van Langevelde, F., Van de Vijver, C.A.D.M., Govender, N. & Prins, H.H.T. (submitted) Clustering of savanna trees reduces damaging effects of fire in South African Savannas.

Groen, T.A., Van Langevelde, F., Van de Vijver, C.A.D.M., Prins, H.H.T., De Raad, A., & De Leeuw, J. (in prep) Abiotic determinants of tree grass patterns in African savannas: a continental analysis.

De Knegt, H.J., Groen, T.A., Van de Vijver, C.A.D.M., Prins, H.H.T. & Van Langevelde, F. (submitted) Herbivores as architects of savannas: inducing and modifying spatial patterning.

Groen, T.A., Van Langevelde, F., Van de Vijver, C.A.D.M. & Prins, H.H.T. (submitted) Dynamic interactions between vegetation and herbivore populations increase the stability of savannas.

PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of Literature (5.6 credits)

- Tree-grass patterns and the processes behind it (2003)

Laboratory Training and Working Visits (4.3 credits)

- First exploration of savanna research South Africa; University of Fort Hare (2004)

Post-Graduate Courses (7 credits)

- Population dynamics; FE (2003)
- Theoretical ecology; FE (2003)
- Spatial and temporal aspects in resource ecology; PE&RC (2005)
- Consumer resource interactions; PE&RC (2007)

Deficiency, Refresh, Brush-up and General Courses (2.8 credits)

- Advanced statistics; PE&RC (2003)
- Survival analysis; PE&RC (2004)

Competence Strengthening / Skills Courses (4.4 credits)

- Time planning and project management; WGS (2004)
- Scientific writing; WGS (2005)
- PhD career perspectives; WGS (2006)
- Writing a grant proposal; WGS (2007)

Discussion Groups / Local Seminars and other Scientific Meetings (9 credits)

- Discussion group 10—Forest ecology and nature conservation (2003-2006)
- Discussion group 9—Mat en stat (2003-2006)
- Current themes in ecology (2003-2006)

PE&RC Annual Meetings, Seminars and the PE&RC Weekend (6.45 credits)

- The young landscape ecologist symposium (2002)
- NVTB AIO day (2003)
- PE&RC day (2003-2006)
- PE&RC weekend (2004 and 2005)

International Symposia, Workshops and Conferences (3.6 credits)

- Dynamics of patterns; Lorenz Institute, Leiden, the Netherlands (2005)
- Kruger network meeting; Scientific Services, Skukuza, South Africa (2006)

Courses in which the PhD Candidate has Worked as a Teacher

- Models for forest and nature management (2003-2006); REG, 20 days
- Animal ecology (2003-2004); REG, 8 days

Supervision of MSc student(s)

- Savanna dynamics; 3 students, 30 days

References

References to chapter 1

Adler, B.P., Raff, D.A. & Lauenroth, W.K. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* **128**: 465-479.

Archer, S.R., Scifres, C., Bassham, C.R. & Maggio, R. 1988. Autogenic succession in a Subtropical Savanna: Conversion of grassland to Thorn Woodland. *Ecological Monographs* **58**: 111-127.

Armstrong, R.A. & McGehee, R. 1980. Competitive exclusion. *American Naturalist* **115**: 151-170.

Belsky, A.J. 1991. Tree/grass ratios in East African savannas: a comparison of existing models. (139-145) in: Werner, P.A. (ed.). Savanna ecology and management: Australian perspectives and intercontinental comparisons. Blackwell, Oxford.

Belsky, A.J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology* **75**: 922-932.

Berjak,S.G. & Hearne, J.W. 2002. An improved cellular automaton model for simulating fire in a spatially heterogeneous Savanna system. *Ecological modelling* **148**: 133-151.

Bond, W. J., Midgley, G. F. & Woodward, W. I. 2003. The importance of low atmospheric CO2 and fire in promoting the spread of grasslands and savannas. *Global Change Biology* **9**: 973-982.

Briggs, J.M., Knapp, A.K. & Brock, B.L. 2002. Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing Interactions. *American Midland Naturalist* **147**: 287-294.

Brown, J.R. & Carter, J. 1998. Spatial and temporal patterns of exotic shrub invasion in an Australian tropical grassland. *Landscape Ecology* **13**: 93-102.

Cid, M.S. & Brizuela, M.A. 1998. Heterogeneity in tall fescue pastures created and sustained by cattle grazing. *Journal of Range Management* **51**: 644-649.

De Ronde, C., Trollope, W.S.W., Parr, C.L., Brockett, B.H. & Geldenhuys, C.J. 2004. Fire effects on flora and fauna. (60-87) in: Goldhammer, J.G. & De Ronde, C. (eds.). Wildland Fire Management: Handbook for Sub-Sahara Africa. Global Fire Monitoring Centre, Freiburg. pp. 432.

Dublin, H.T., Sinclair, A.R.E. & McGlade J. 1990. Elephants and fire as causes of multiple stable states in the serengeti-mara woodlands. *Journal of Animal Ecology* **59**: 1147-1164.

Folke, C., Carpenter, S.R., Walker, B.H., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C.S. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Reviews of Ecology, Evolution and Systematics* **35**: 557-581.

Fortin, M.J. & Dale, M. 2005. Spatial analysis; a guide for ecologists. Cambridge university press, Cambridge, UK. pp. 365.

Gierer, A. 1981. Generation of biological patterns and form: some physical, mathematical, and logical aspects. *Progress in Biophysics and Molecular Biology* **37**: 1-47.

Gillson, L. & Hoffman, M.T. 2007. Rangeland ecology in a changing world. *Science* **315**: 53-54.

Hoffmann, W.A., Schroeder, W. & Jackson, R.B. 2002. Positive feedbacks of fire, climate, and vegetation and the conversion of tropical savanna. *Geophysical Research Letters* 29:doi:10.1029/2002GL015424.

Janssen, M.A., Anderies, J.M. and Walker, B.H. 2004. Robust strategies for managing rangelands with multiple stable attractors. *Journal of environmental economics and management* **47**: 140-162.

Jeltsch, F., Weber, G.E. & Grimm, V. 2000. Ecological buffering mechanisms in savannas: A unifying theory of long-term tree-grass coexistence. *Plant Ecology* **161**: 161-171.

Knoop, W.T. & Walker, B.H. 1985. Interactions of woody and herbaceous vegetation in a southern african savanna. *Journal of Ecology* **73**: 235-253.

Law, R., Dieckmann, U. & Metz, J.A.J. 2000. Introduction. (1-10) in Dieckmann, U. Law, R. and Metz, J.A.J. The geometry of Ecological interactions, simplifying spatial complexity. Cambridge University press, Cambridge, UK. pp. 564.

May, R.M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* **269**: 471-477.

Meinhardt, H. 2003. The algorithmic beauty of sea shells. Springer, Germany.

Noy-Meir, I. 1975. Stability of grazing systems: an application of predator-prey graphs. *Journal of Ecology* **63**: 459-481.

Rietkerk, M, Ketner, P., Stroosnijder, L. & Prins, H.H.T. 1996. Sahelian rangeland development: a catastrophe?'. *Journal of Range Management* **49**: 512-519.

Rietkerk, M., Dekker, S.C., De Ruiter, P.C. & Van de Koppel, J. 2004. Self-Organized Patchiness and Catastrophic Shifts in Ecosystems. *Science* **305**: 1926-1929.

Rietkerk, M. & Van de Koppel, J. 1997. Alternate stable states and threshold effects in semi-arid grazing systems. *Oikos* **79**: 69-76.

Roques, K.G., O'Connor, T.G. & Watkinson, A.R. 2001. Dynamics of shrub encroachment in an African savanna: relative influence of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* **38**: 268-280.

Sala, O. E. et al. 2000. Biodiversity-global biodiversity scenarios for the year 2100. *Science* **287**: 1770-1774.

Sankaran, M., Ratnam, J. & Hanan, N.P. 2004. Tree–grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters* **7**: 480-490.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J. & Zambatis, N. 2005. Determinants of woody cover in African savannas. *Nature* **438**: 846-849.

Scheffer, M., Carpenter, S.R., Foley, J.A., Folke, C. & Walker, B.H. 2001. Catastrophic shifts in ecosystems. *Nature* **413**: 591-596.

Schenk, H.J. & Jackson, R.B. 2002. Rooting depth, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology* **90**: 480-494.

Scholes, R.J. & Archer, S.R. 1997. Tree-Grass interactions in savannas. *Annual Reviews of Ecological Systems* **28**: 517-544.

Scholes, R.J. & Walker, B.H. 1993. An African savanna: synthesis of the nylsvley Study. Cambridge University Press., Cambridge UK.

Schröder, A., Persson, L. & De Roos, A.M. 2005. Direct experimental evidence for alternative stable states: a review. *Oikos* **110**: 3-19.

Shea, R.W., Shea, B.W., Kauffman, J.B., Ward, D.E., Haskins, C.I. & Scholes, M.C. 1996. Fuel biomass and consumption factors associated with fires in savanna ecosystems of South Africa and Zambia. *Journal of Geophysical Research* **101**: 23551-23568.

Thom, R. 1975. Structural stability and morphogenesis: an outline of a general theory of models. Benjamin Cummings, Reading.

Tilman, D. & Kareiva, P. 1997. Spatial ecology; the role of space in population dynamics and interspecific interactions. Princeton university press, Princeton, New Jersey, USA. pp. 368 + xiv.

Tilman, D., Lehman, C.L. & Kareiva, P. 1997. Population Dynamics in Spatial Habitats (3-20) in Tilman, D. and Kareiva, P. Spatial ecology; the role of space in population dynamics and interspecific interactions. Princeton university press, Princeton, New Jersey, USA. pp. 368 + xiv.

Van Auken, O.W. 2000. Shrub invasions of north american semiarid grasslands. *Annual Review of Ecology and Systematics* **31**: 197-215.

Van de Koppel, J., Rietkerk, M. & Weissing, F.J. 1997. Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends in Ecology and Evolution* **12**: 352-356.

Van de Koppel, J. & Rietkerk, M. 2004. Spatial interactions and resilience in arid ecosystems. *American Naturalist* **163**: 113-121.

Van de Vijver, C.A.D.M. 1999. Fire and life in Tarangire. Effects of burning and Herbivory on an East African Savanna System, Thesis, Wageningen University, Wageningen.

Van Langevelde, F., Van de Vijver, C.A.D.M., Kumar, L., Van de Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J., Prins, H.H.T. & Rietkerk, M. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**: 337-350.

Van Nes, E.H. & Scheffer, M. 2005. Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. *Ecology* **86**: 1797-1807.

Walker, B.H., Ludwig, D., Holling, C.S. & Peterman, R.M. 1981. Stability of semi-arid savanna grazing systems. *Journal of Ecology* **69**: 473-498.

Walker, B.H. & Noy-Meir, I. 1982. Aspects of the stability and resilience of savanna ecosystems. (556-590) in: Huntley, B.J. & Walker, B.H. (eds.). Ecology of Tropical Savannas. Springer Verlag, Berlin.

Walter, H., 1971. Ecology of Tropical and Subtropical Vegetation. Oliver & Boyd, Edinburgh, UK.

Zeeman, E.C. 1976. Catastrophe theory. *Scientific American* **234**: 65-83.

References to chapter 2

Archer, S. 1989. Have southern Texas savannas been converted to woodland in recent history? *American Naturalist* **134**: 545-561.

Archer, S. 1990. Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, U.S.A. *Journal of biogeography* **17**: 453-462.

Barbosa P.M., Stroppiana, D. Grégoire J-M. & Pereira, J.M.C. 1999. An assessment of vegetation fire in Africa (1981-1991): burned areas, burned biomass and atmospheric emissions. *Global Biogeochemical Cycles* **13**: 933-950.

Batjes, N.H. 2005. ISRIC-WISE global data set of derived soil properties on a 0.5 by 0.5 degree grid (Version 3.0). Report number: 2005/08, ISRIC-World Soil Information.

Bond, W.J. & Keeley, J.E. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* **20**: 387-394.

Brown, J.R. & Carter, J. 1998. Spatial and temporal patterns of exotic shrub invasion in an Australian tropical grassland. *Landscape Ecology* **13**: 93-102.

Caylor, K.K., Shugart, H.H., Dowty, P.R. & Smith, T.M. 2003. Tree spacing along the Kalahari transect in southern Africa. *Journal of Arid Environments* **54**: 281-296.

Chevan, A. & Sutherland, M. 1991. Hierarchical partitioning. *The American Statistician* **45**: 90-96.

Couteron, P. & Lejeune, O. 2001. Periodic spotted patterns in semi-arid vegetation explained by a propagation-inhibition model. *Journal of Ecology* **89**: 616-628.

Eamus, D., O'Grady, A.P. & Hutley, L. 1999. Dry season conditions determine wet season water use in the wet-dry tropical savannas of northern Australia. *Tree physiology* **20**: 1219-1226.

Falling Rain 2006 Worldwide rainfall data. Available at http://www.fallingrain.com/world/index.html.

FAO GeoNetwork, environmental and natural resources. Available at http://www.fao.org/geonetwork/srv/en/main.home.

Goheen, J.R., Young, T.P., Keesing, F. & Palmer, T.M. 2007. Consequences of herbivory by native ungulates for the reproduction of a savanna tree. *Journal of Ecology* **95**: 129-138.

Higgins, S.I., Bond, W.J. & Trollope, W.S.W. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* **88**: 213-229.

Jeltsch, F., Milton, S.J., Dean, W.R.J. & Van Rooyen, N. 1996. Tree spacing and coexistence in semiarid savannas. *Journal of Ecology* **84**: 583-595.

Jeltsch, F., Milton, S.J., Dean, W.R.J., Van Rooyen, N. & Moloney, K.A. 1998. Modelling the impact of small-scale heterogeneities on tree-grass coexistence in semi-arid savannas. *Journal of Ecology* **86**: 780-793.

Jeltsch, F., Weber, G.E. & Grimm, V. 2000. Ecological buffering mechanisms in savannas: A unifying theory of long-term tree-grass coexistence. *Plant Ecology* **161**: 161-171.

Koenker, R.W. 2006. Quantreg: Quantile Regression. R package version 4.05. Available at http://www.r-project.org.

Koenker, R.W. & Bassett, G.W. 1978. Regression quantiles. *Econometrica* **46**: 33-50.

LandScanTM 2005 Global Population Database. Oak Ridge, TN: Oak Ridge National Laboratory. Available at http://www.ornl.gov/landscan/.

Lejeune, O., Couteron, P. & Lefever, R. 1999. Short range co-operativity competing with long range inhibition explains vegetation patterns. *Acta Oecologica* **20**: 171-183.

Lejeune, O., Tlidi, M. & Couteron, P. 2002. Localized vegetation patches: A self-organized response to resource scarcity. *Physical Review* E 66.

Ludwig, F., De Kroon, H., Berendse, F. & Prins, H.H.T. 2004. The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant Ecology* **170**: 93-105.

Ludwig, J.A., Tongway, D.J. & Marsden, S.G. 1999. Stripes, strands or stipples: modelling the influence of three landscape banding patterns on resource capture and productivity in semi-arid woodlands, Australia. *Catena* **37**: 257-273.

McGarigal, K. & Marks, B.J. 1993. Fragstats: Spatial pattern analysis program for quantifying landscape structure. Report number: Forest Science Department, Oregon State University.

Prins, H.H.T. & Beekman, J.H. 1989. A balanced diet as a goal for grazing: The food of the Manyara buffalo. *African Journal of Ecology* **27**: 241-259.

Prins, H.H.T. & Van der Jeugd, H.P. 1993. Herbivore population crashes and woodland structure in East Africa. *Journal of ecology* **81**: 305-314.

Quinn, G.P. & Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press. pp. 537.

Rietkerk, M., Boerlijst, M.C., Van Langevelde, F., HilleRisLambers, R., Van de Koppel, J., Kumar, L., Prins, H.H.T. & De Roos, A.M. 2002. Self organisation of vegetation in Arid Ecosystems. *American Naturalist* **160**: 524-530.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J. & Zambatis, N. 2005. Determinants of woody cover in African savannas. *Nature* **438**: 846-849.

Scholes, R.J. & Archer, S.R. 1997. Tree-Grass interactions in savannas. *Annual Reviews of Ecological Systems* **28**: 517-544.

Smith, T.M. & Goodman, P.S. 1986. The Effect of Competition on the Structure and Dynamics of Acacia Savannas in Southern Africa. *Journal of Ecology* **74**: 1031-1044.

Tilman, D. & Kareiva, P. 1997. Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton. pp. 368.

Trollope, W.S.W. 1984. Fire in Savanna. (199-218) in: Booysen, P.D.V. & Tainton, N.M. (eds.). Ecological effects of fire of southern African ecosystems. Springer Verlag, Berlin.

USGS 2005 Africa land cover characteristics data base. Available at http://edcsns17.cr.usgs.gov/glcc/afdoc2_0.html.

Van de Koppel, J. & Rietkerk, M. 2004. Spatial interactions and Resilience in Arid Ecosystems. *American Naturalist* **163**: 113-121.

Van der Brink, P.J. & Ter Braak, C.J.F. 1998. Multivariate analysis of stress in experimental ecosystems by Principal Response Curves and similarity analysis. *Aquatic ecology* **32**: 163-178.

Van Langevelde, F., Van de Vijver, C.A.D.M., Kumar, L., Van de Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J., Prins, H.H.T., & Rietkerk, M. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**: 337-350.

Wagner, H.H. & Fortin, M.J. 2005. Spatial analysis of landscapes: concepts and statistics. *Ecology* **86**: 1975-1987.

Walsh, C.J. 2004. Hier.part: Hierarchical Partitioning. R package version 1.0-1. Available at http://www.r-project.org.

Walker, B.H. & Noy-Meir, I. 1982. Aspects of the stability and resilience of savanna ecosystems. (556-590) in: Huntley, B.J. & Walker, B.H. (eds.). Ecology of Tropical Savannas. Springer Verlag, Berlin.

Walter, H. 1971. Ecology of Tropical and Subtropical Vegetation. Oliver & Boyd, Edinburgh, UK.

Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* **3**: 85-397.

References to chapter 3

Achibald, S., Bond, W.J., Stock, W.D. & Fairbanks, D.H.K. 2004. Shaping the landscape: fire–grazer interactions in an African savanna. *Ecological Applications* **15**: 96-109.

Berjak, S.G. & Hearne, J.W. 2002. An improved cellular automaton model for simulating fire in a spatially heterogeneous Savanna system. *Ecological Modelling* **148**: 133-151.

Biggs, R., Biggs, H.C., Dunne, T.T., Govender, N. & Potgieter, A.L.F. 2003. Experimental burn plot trial in the Kruger National Park: history, experimental design and suggestions for data analysis. *Koedoe* **46**: 1-15.

Carrick, P.J. 2003. Competitive and facilitative relationships among tree shrub species and the role of browsing intensity and rooting depth in the succulent Karoo, South Africa. *Journal of vegetation science* **14**: 761-772.

De Ronde, C., Trollope, W.S.W., Parr, C.L., Brockett, B.H. & Geldenhuys, C.J. 2004. Fire effects on flora and fauna. (60-87) in: Goldhammer, J.G. & De Ronde, C. (eds.). *Wildland Fire Management: Handbook for Sub-Sahara Africa*. Global Fire Monitoring Centre, Freiburg. pp. 448.

Euroconsult 1989. *Agricultural compendium for rural development in the tropics and subtropics*. Elsevier, Amsterdam. 740 pp.

Gertenbach, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe* **26**: 9-121.

Gibbs Russel, G.E., Watson, L., Koekemoer, M., Smook, L., Barker, N.P., Anderson, H.M., & Dallwitz, M.J. 1990. *Grasses of Southern Africa*. National Botanic Gardens/Botanical Research Institute, South Africa. pp. 437.

Gignoux, J., Menaut, J.C., Noble, I.R., & Davies, I.D. 1998. A spatial model of savanna function and dynamics: model description and preliminary results. (361-383) in: Newbery, D.M., Prins, H.H.T., & Brown, N. (eds.). *Dynamics of Tropical Communities*. Blackwell, London. 635 pp.

Gignoux, J., Noble, I.R., & Menaut, J.C. 1995. Modelling tree community dynamics in savannas: effects of competition with grasses and impact of disturbance. (219-230) in Bellan-Santini, D., Bonin, G., & Emig, C. (eds.). *Functioning and dynamics of natural and perturbed ecosystems*. Intercept Ltd, Paris.

Govender, N., Trollope, W.S.W., & Van Wilgen, B.W. 2006. The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology* **43:** 748-758.

Goheen, J.R., Young, T.P., Keesing, F. & Palmer, T.M. 2007. Consequences of herbivory by native ungulates for the reproduction of a savanna tree. *Journal of Ecology* **95:** 129-138.

Hines, W.G.S. & Hines, R.J.O. 1979. The Eberhardt statistic and the detection of nonrandomness of spatial point distributions. *Biometrika* **66**: 73-79.

Hoffman, W.A., Orthen, B., Kielse, P., & Do Nascimento, V. 2003. Comparative fire ecology of tropical savanna and forest trees. *Functional Ecology* **17**: 720-726.

Jeltsch, F., Milton, S.J., Dean, W.R.J. & Van Rooyen, N. 1996. Tree spacing and coexistence in semiarid savannas. *Journal of Ecology* **84**: 583-595.

Jeltsch, F., Milton, S.J., Dean, W.R.J., Van Rooyen, N. & Moloney, K.A. 1998. Modelling the impact of small-scale heterogeneities on tree-grass coexistence in semi-arid savannas. *Journal of Ecology* **86**: 780-793.

Joquet, P., Tavernier, V., Abbadie, L. & Lepage, M. 2005. Nests of subterranean fungus-growing termites (Isoptera, Macrotermitinae) as nutrient patches for grasses in savannah ecosystems. *African Journal of Ecology* **43**: 191-196.

Kennedy, A.D. & Potgieter, A.L.F. 2003. Fire season affects size and architecture of *Colophospermum mopane* in southern African savannas. *Plant ecology* **167**: 179-193.

Knp Scientific Services 2005. Kruger Climate, available at http://www.sanparks.org/parks/kruger/conservation/scientific/faq/KNP_Seasons.pdf.

Marion, G., Swain, D.L. & Hutchings, M.R. 2004. Understanding foraging behaviour in spatially heterogeneous environments. *Journal of Theoretical Biology* **292**: 127-142.

Pacala, S.W. & Levin, S.A. 1997. Biologically Generated Spatial Pattern and the Coexistence of Competing Species. (204-232) in Tilman, D. & Kareiva, P. (eds.). *Spatial ecology: The role of space in population dynamics and interspecific interactions.* Princeton University Press, Princeton. 368 pp.

Prins, H.H.T. & Van der Jeugd, H.P. 1993. Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology* **81**: 305-314.

Rietkerk, M., Boerlijst, M.C., Van Langevelde, F., HilleRisLambers, R., Van de Koppel, J., Kumar, L., Prins, H.H.T. & De Roos, A.M. 2002. Self organisation of vegetation in Arid Ecosystems. *American Naturalist* **160**: 524-530.

Rietkerk, M., Dekker, S.C., De Ruiter, P.C., & Van de Koppel, J. 2004. Self-Organized Patchiness and Catastrophic Shifts in Ecosystems. *Science* **305**: 1926-1929.

Scholes, R.J. & Archer, S.R. 1997. Tree-Grass interactions in savannas. *Annual Reviews of Ecological Systems* **28**: 517-544.

Shea, R.W., Shea, B.W., Kauffman, J.B., Ward, D.E., Haskins, C.I., & Scholes, M.C. 1996. Fuel biomass and consumption factors associated with fires in savanna ecosystems of South Africa and Zambia. *Journal of Geophysical Research* **101**: 23551-23568.

Smith, T.M. & Goodman, P.S. 1986. The Effect of Competition on the Structure and Dynamics of Acacia Savannas in Southern Africa. *Journal of Ecology* **74**: 1031-1044.

Tainton, N.M. 1999. *Veld management in South Africa.* University of Natal Press, Pietermaritzburg, South Africa. 472 pp.

Van de Vijver, C.A.D.M., Foley, C.A., & Olff, H. 1999. Changes in the woody component of an East African savanna during 25 years. *Journal of Tropical Ecology* **15**: 545-564.

Van Langevelde, F., Van de Vijver, C.A.D.M., Kumar, L., Van de Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J., Prins, H.H.T. & Rietkerk, M. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**: 337-350.

Van Nes, E.H. & Scheffer, M. 2005. Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. *Ecology* **86**: 1797-1807.

Wessels, D. 2001. *Mopane Woodland management*. University of the North, South Africa. Report number R7822. 14 pp.

Zar, J.H. 1996. *Biostatistical analysis*. Prentice-Hall, Upper Saddle River. 931 pp.

References to box 3.1

Bond, W.J. & Keeley, J.E., 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* **20**: 387-394.

Bond, W.J. & Van Wilgen, B.W. 1996. Fire and Plants. Chapman & Hall, London. pp. 263.

De Ronde, C., Trollope, W.S.W., Parr, C.L., Brockett, B.H., & Geldenhuys, C.J., 2004. Fire effects on flora and fauna. (60-87) in Goldhammer, J.G. & De Ronde, C. (eds.). Wildland Fire Management: Handbook for Sub-Sahara Africa. Global Fire Monitoring Centre, Freiburg.

Govender, N., Trollope, L.A. & Wilgen, B.W. 2006. The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology* **43**: 748-758.

Hoffman, W.A., Orthen, B., Kielse, P. & Do Nascimento, V. 2003. Comparative fire ecology of tropical savanna and forest trees. *Functional Ecology* **17**: 720-726.

Shea, R.W., Shea, B.W., Kauffman, J.B., Ward, D.E., Haskins, C.I. & Scholes, M.C. 1996. Fuel biomass and consumption factors associated with fires in savanna ecosystems of South Africa and Zambia. *Journal of Geophysical Research* **101**: 23551-23568.

Trollope, W.S.W., De Ronde, C. & Geldenhuys, C.J. 2004. Fire behaviour. (27-59) in Goldhammer, J.G. & De Ronde, C. (eds.). Wildland Fire Management: Handbook for Sub-Sahara Africa. Global Fire Monitoring Centre, Freiburg.

Van Langevelde, F., Van de Vijver, C.A.D.M., Kumar, L., Van de Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J., Prins, H.H.T. & Rietkerk, M. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**: 337-350.

References to chapter 4

Adler, P.B., Raff, D.A. & Lauwenroth, W.K. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* **128:** 465-479.

Archer, S. 1990. Development and stability of grass/woody mosaic in a subtropical savanna parkland, Texas, U.S.A. *Journal of Biogeography* **17**: 453-462.

Archer, S.R., Scifes, C. & Bassham, C.R. 1988 Autogenic succession in a sub-tropical savanna: conversion of grassland to Thorn woodland. *Ecological Monographs* **58**: 111-127.

Augustine, D.J. & McNaughton, S.J. 2004. Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology* **41**: 45-58.

Bailey, D.W., Gross, J.E., Laca, E.A., Rittenhouse, L.R., Coughenour, M.B., Swift, D.M. & Sims, P.L. 1996. Mechanism that result in large herbivore grazing distribution patterns. *Journal of Range Management* **49**: 386-400.

Bakker, J.P., De Leeuw, J. & Van Wieren, S.E. 1984. Micro patterns in grassland vegetation created and sustained by sheep grazing. *Vegetatio* **55**: 153-161.

Baraza, E., Zamora, R. & Hódar, J.A. 2006. Conditional outcomes in plant/herbivore interactions: neighbours matter. *Oikos* **113:** 148-156.

Breshears, D.D. 2006. The grassland-forest continuum: trends in ecosystem properties for woody plant mosaics? *Frontiers in Ecology and Environmental Sciences* **4**: 96-104.

Briggs, J.M., Knapp, A.K. & Brock, B.L. 2002. Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing Interactions. *American Midland Naturalist* **147**: 287-294.

Bond, W. J., Midgley, G. F. & Woodward, W. I. 2003. The importance of low atmospheric CO2 and fire in promoting the spread of grasslands and savannas. *Global Change Biology* **9**: 973-982.

Caylor, K.K & Shugart, H.H. 2004. Simulated productivity of heterogeneous patches in Southern African savanna landscapes using a canopy productivity model. *Landscape Ecology* **19**: 401-415.

Cid, M.S. & Brizuela, M.A. 1998. Heterogeneity in tall fescue pastures created and sustained by cattle grazing. *Journal of Range Management* **51**: 644-649.

Coppock, D.L., Detling, J.K., Ellis, J.E. & Dyer, M.I. 1983. Plant-Herbivore Interactions in a North American Mixed-Grass Prairie: I. Effects of Black-Tailed Prairie Dogs on Intraseasonal Aboveground Plant Biomass and Nutrient Dynamics and Plant Species Diversity. *Oecologia* **56**: 1-9.

Coughenour, M.B. 1991. Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. *Journal of Range Management* **44**: 530-542.

Couteron, P. & Kokou, K. 1997. Woody vegetation spatial patterns in a semi-arid savanna of Burkina Faso, West Africa. *Plant Ecology* **132**: 211-227.

Crampton, E.W. & Harris, J.E. 1969 *Applied animal nutrition: the use of feedstuffs in the formulation of livestock rations*. W.H. Freeman, USA.

De Ridder, N. & Van Keulen, H. 1995. Estimating biomass through transfer functions based on simulation model results: a case study for the Sahel. *Agricultural Water Management* **28**: 57-71.

Du Toit, J.T., Bryant, J.P. & Frisby, K. 1990. Regrowth and palatability of acacia shoots following pruning by African savanna browsers. *Ecology* **71**: 149-154.

Drescher, M., Heitkönig, I.M.A., Van den Brink, P.J. & Prins H.H.T. 2006. Effects of sward structure on herbivore foraging behaviour in a South African savanna: An investigation of the forage maturation hypothesis. *Austral Ecology* **31**: 76-87.

Eagleson, P.S. & Segara, R.I. 1985. Water-limited equilibrium of savanna vegetation systems. *Water Resource Research* **21**: 1483-1493.

Eagleson, P.S. 1989. Stability of tree/grass vegetation systems. (109-113) in Berger, A., Dickinson, R.E. & Kidson, J.W. (eds.). *Understanding climate change.* Geophysical Monographs 52, Geophysical Union, Washington.

Fernandez-Illescas, C.P. & Rodriguez-Iturbe, I. 2003. Hydrologically driven hierarchical competition-colonization models: the impact of interannual climate fluctuations. *Ecological Monographs* **73**: 207-222.

Fornara & Du Toit 2007. Browsing lawns? responses of acacia nigrescens to ungulate browsing in an african savanna. *Ecology* **88**: 200-209.

Fretwell, S.D. & Lucas, H.I. 1970. On territorial behavior and other factors influencing distribution in birds. I. Theoretical development. *Acta Biotheoretica* **19**: 16-36.

Gambiza, J., Bond, W.J., Frost, P. G. H. & Higgins, S. 2000. Land use options in dry tropical woodland ecosystems in Zimbabwe. *Ecological Economics* **33**: 353-368.

Greig-Smith, P. 1979. Pattern in Vegetation. *Journal of Ecology* **67**: 775-779.

Higgins, S.I., Bond, W.J. & Trollope, W.S.W 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* **88**: 213-229.

Hobbs, N.T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* **60**: 695-713.

Hobbs, N.T. 1999. Responses of large herbivores to spatial heterogeneity in ecosystems. (97-129) in H.G. Jung & G.C. Fahey (eds.) *Nutritional ecology of herbivores: Proceedings of the 5th International Symposium on the Nutrition of Herbivores*. American Society of Animal Science, Savory, Ill.

Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* **91**: 385-398.

House, J.I., Archer, S., Breshears, D.D. & Scholes, R.J. 2003. Conundrums in mixed woody–herbaceous plant systems. *Journal of Biogeography* **30**: 1763-1777.

Huisman, J., Grover, J.P., Van der Wal, R. & Van Andel, J. 1997. Competition for light, plant-species replacement and herbivore abundance along productivity gradients. (239-269) in H. Olff, V.K. Brown, & R.H. Drent (eds.) *Herbivores: Between plants and predators*. Blackwell Science Ltd., UK.

Huntley, B.J. & Walker, B.H. 1982. *Ecology of tropical savannas*. Springer-Verlag, New York.

Jefferies, R.L., Klein, D.R. & Shaver, G.R. 1994. Vertebrate herbivores and northern plant communities: reciprocal influences and responses. *Oikos* **71:** 193-206.

Jeltsch, F., Milton, S.J., Dean, W.R.J. & Van Rooyen, N. 1996. Tree spacing and coexistence in semiarid savannas. *Journal of Ecology* **84**: 583-595.

Jeltsch, F., Milton, S.J., Dean, W.R.J., Van Rooyen, N. & Moloney, K.A. 1998. Modeling the impact of small-scale heterogeneities on tree-grass coexistence in semi-arid savannas. *Journal of Ecology* **86**: 780-793.

Jeltsch, F., Weber, G.E. & Grimm, V. 2000. Ecological buffering mechanisms in savannas: a unifying theory of long-term tree-grass coexistence. *Plant Ecology* **161**: 161-171.

Klausmeier, C.A. 1999. Regular and irregular patterns in semiarid vegetation. *Science* **284**: 1826-1828.

Lamprey, H.F., Herlocker, D.J. & Field, C.R. 1980. Report on the state of knowledge on browse in East Africa in 1980. in Le Houérou H.N.(ed.) *Browse in Africa: the current state of knowledge*. International Livestock Centre for Africa, Addis Ababa, Ethiopia.

Le Houérou, H.N. 1980. *Browse in Africa: the current state of knowledge*. International Livestock Centre for Africa, Addis Ababa, Ethiopia.

Lee J.E., Oliveira, R.S. Dawson, T.E. & Fung, I. 2005. Root functioning modifies seasonal climate. *Proceedings of the National Academy of Sciences* **102**: 17576-17581.

Lejeune, O., Tlidi, M. & Couteron, P. 2002. Localized vegetation patches: a self-organized response to resource scarcity. *Physical Review E* **66:** 010901.

Ludwig, F., Dawson, T.E., de Kroon, H., Berendse, F. & Prins, H.H.T. 2003. Hydraulic lift in Acacia tortilis trees on an East African savanna. *Oecologia* **134:** 293-300.

McNaughton, S.J. 1984. Grazing lawns: animals in herds, plant form and coevolution. *American Naturalist* **124**: 863-886.

Murwira, A. & Skidmore, A.K. 2005. The response of elephants to the spatial heterogeneity of vegetation in a Southern African agricultural landscape. *Landscape Ecology* **20**: 217-234.

Murwira, A. 2003. Scale matters: a new approach to quantify spatial heterogeneity for predicting the distribution of wildlife. PhD thesis, Wageningen University, The Netherlands.

Owen-Smith, R.N. 2002. Adaptive Herbivore Ecology. From Resources to Populations in Variable Environments. Cambridge University Press, UK.

Pellew, R.A.P. 1983. The impact of elephant, giraffe and fire upon the *Acacia tortilitis* woodlands of the Serengeti. *African Journal of Ecology* **21**: 41-74.

Prins, H.H.T. & Douglas-Hamilton, I. 1990. Stability in a multi-species assemblage of large herbivores in East Africa. *Oecologia* **83**: 392-400.

Prins, H.H.T. & Van der Jeugd, H. 1993. Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology* **81**: 305-314.

Prins, H.H.T. & Olff, H. 1998. Species-richness of African grazer assemblages: towards a functional explanation. In D.M. Newberry, H.H.T. Prins & N.D. Brown (eds.). *Dynamics of tropical communities*. Blackwell Science Ltd., UK.

Richards, C.R., Haenlein, G.F.W., Calhoun, M.C., Connolly, J.D. & Weaver, H.G. 1962. Date of cut vs. the combination of crude fiber and crude protein as estimators of forage quality. *Journal of Animal Science* **21**: 844-847.

Rietkerk, M., Boerlijst, M.C., Van Langevelde, F., HilleRisLambers, R., Van de Koppel, J., Kumar, L., Prins, H.H.T., De Roos, A.M. 2002. Self organisation of vegetation in Arid Ecosystems. *American Naturalist* **160**: 524-530.

Rietkerk, M., Dekker, S.C., De Ruiter, P.C. & Van de Koppel, K.J. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. *Science* **305**: 1926-1929.

Roques, K.G., O'Connor, T.G. & Watkinson, A.R. 2001. Dynamics of shrub encroachment in an African savanna: relative influence of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* **38**: 268-280.

Sala, O. E. *et al.* 2000. Biodiversity-global biodiversity scenarios for the year 2100. *Science* **287**: 1770-1774.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J. & Zambatis, N. 2005. Determinants of woody cover in African savannas. *Nature* **438**: 846-849.

Sankaran, M., Ratnam, J. & Hanan, N.P. 2004. Tree–grass coexistence in savannas revisited - insights from an examination of assumptions. *Ecology Letters* **7**: 480-490.

Schenk, H.J. & Jackson, R.B. 2002. Rooting depths, lateral root spreads and below-ground above-ground allometries of plants in water-limiting ecosystems. *Journal of Ecology* **90**: 480-494.

Scholes, R.J. & Archer, S. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* **28**: 517-544.

Scholes, R.J. & Walker, B.H. 1993. An African savanna: synthesis of the Nylsvley study. Cambridge University Press, UK.

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. & Swift, D.M. 1986. Large herbivore foraging and ecological hierarchies: landscape ecology can enhance traditional foraging theory. *BioScience* **37**: 789-799.

Stephens, D. W. & Krebs, J. R. 1986. Foraging Theory. Princeton University Press, Princeton.

Treitz, P. & Howarth, P. 2000. High spatial resolution remote sensing data for forest ecosystem classification: an examination of spatial scale. *Remote Sensors Environment* **72**: 268-289.

Van de Koppel, J. & Prins, H.H.T. 1998. The importance of herbivore interactions for the dynamics of African savanna woodlands: an hypothesis. *Journal of Tropical Ecology* **14**: 565-576.

Van Langevelde, F., Van de Vijver, C.A.D.M., Kumar, L., Van de Koppel, J., De Ridder, N., Van Andel, J. Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J., Prins, H.H.T. & Rietkerk, M. 2003. Effect of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**: 337-350.

Van Wijk, M.V. & Rodriguez-Iturbe, I. 2002. Tree-grass competition in space and time: insights from a simple cellular automata model based on ecohydrological dynamics. *Water Resources Research* **38:** 1179.

Walker, B.H., Ludwig, D., Holling, C.S. & Peterman, R.M. 1981. Stability of semi-arid savanna grazing systems. *Journal of Ecology* **69**: 473-498.

Walker, B.I. & Noy-Meir, I. 1982. Aspects of stability and resilience of savanna ecosystems. (577-590) in Huntley B.J. & Walker B.H. (eds.). *Ecology of tropical savannas.* Springer-Verlag, Berlin, Germany.

Walter, H. 1971. *Ecology of tropical and subtropical vegetation*. Oliver & Boyd, Edinburgh, UK.

Weber, G.E. & Jeltsch, F. 2000. Long-term impacts of livestock herbivory on herbaceous and woody vegetation in semiarid savannas. *Basic and Applied Ecology* **1**: 13-23.

Weltzin, J.F. & McPherson, G.R. 1997. Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, USA. *Oecologia* **112**: 156–164.

Woolnough, A.P. & Du Toit, J.T. 2001. Vertical zonation of browse quality in tree canopies exposed to a size-structured guild of African browsing ungulates. *Oecologia* **129**: 585-590.

References to chapter 5

Archer, S. 1989. Have southern Texas savannas been converted to woodland in recent history? *American Naturalist* **134**: 545-561.

Archer, S. 1990. Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, U.S.A. *Journal of Biogeography* **17:** 453-462.

Archer, S., Scifres, C., Bassham, C.R. & Maggio, R. 1988. Autogenic succession in a subtropical savanna: Conversion of grassland to thorn woodland. *Ecological Monographs* **58**: 111-127.

Baraza, E., Zamora, R. & Hodar, J.A. 2006. Conditional outcomes in plant-herbivore interactions: neighbours matter. *Oikos* **113**: 148-156.

Breshears, D.D. 2006. The grassland-forest continuum: Trends in ecosystem properties for woody plant mosaics? *Frontiers in Ecology and the Environment* **4**: 96-104.

Briggs, J.M., Knapp, A.K. & Brock, B.L. 2002. Expansion of woody plants in tallgrass prairie: A fifteen-year study of fire and fire-grazing interactions. *American Midland Naturalist* **147**: 287-294.

Couteron, P. 2002. Quantifying change in patterned semi-arid vegetation by Fourier analysis of digitized aerial photographs. *International Journal of Remote Sensing* **23**: 3407-3425.

Couteron, P. & Lejeune, O. 2001. Periodic spotted patterns in semi-arid vegetation explained by a propagation-inhibition model. *Journal of Ecology* **89**: 616-628.

Edelstein-Keshet, L. 1988. *Mathematical models in biology*. McGraw-Hill, New York, USA.

Gascoigne, J.C., Beadman, H.A., Saurel, C. & Kai, M.J. 2005. Density dependence, spatial scale and patterning in sessile biota. *Oecologia* **145**: 371-381.

HilleRisLambers, R., Rietkerk, M., Van den Bosch, F., Prins, H.H.T. & De Kroon, H. 2001. Vegetation patters formation in semi-arid grazing systems. *Ecology* **82**: 50-61.

Holmes, E.E., Lewis, M.A., Banks, J.E. & Veit, R.R. 1994. Partial differential equations in ecology: Spatial interactions and population dynamics. *Ecology* **75**: 17-29.

Jeltsch, F., Milton, S.J., Dean, W.R.J. & Van Rooyen, N. 1996. Tree spacing and coexistence in semiarid savannas. *Journal of Ecology* **84**: 583-595.

Jeltsch, F., Milton, S.J., Dean, W.R.J. & Van Rooyen, N. 1997. Simulated pattern formation around artificial waterholes in the semi-arid Kalahari. *Journal of Vegetation Science* **8**: 177-188.

Jeltsch, F., Milton, S.J., Dean, W.R.J., Van Rooyen, N. & Moloney, K.A. 1998. Modelling the impact of small-scale heterogeneities on tree-grass coexistence in semi-arid savannas. *Journal of Ecology* **86**: 780-793.

Klausmeier, C.A. 1999. Regular and irregular patterns in semiarid vegetation. *Science* **284**: 1826-1828.

Lejeune, O., Couteron, P. & Lefever, R. 1999 Short range co-operativity with long range inhibition explains vegetation patterns. *Acta Oecologica* **20**: 171-183.

Lejeune, O., Tlidi, M. & Couteron, P. 2002. Localized vegetation patches: A self-organized response to resource scarcity. *Physical Review* **66**: 1-4.

Lejeune, O., Tlidi, M. & Lefever, R. 2004. Vegetation spots and stripes: Dissipative structures in arid landscapes. *International Journal of Quantum Chemistry* **98**: 261-271.

Loth, P.E., De Boer, W.F., Heitkönig, I.M.A. & Prins, H.H.T. 2005. Germination strategy of the East African savanna tree *Acacia tortilis*. *Journal of Tropical Ecology* **21**: 509-518.

Ludwig, F., De Kroon, H., Berendse, F. & Prins, H.H.T. 2004. The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant Ecology* **170**: 93-105.

Ludwig, J.A., Tongway, D.J. & Marsden, S.G. 1999. Stripes, strands or stipples: modelling the influence of three landscape banding patterns on resource capture and productivity in semi-arid woodlands, Australia. *Catena* **37**: 257-273.

Menaut, J.C., Gignoux, J., Prado, C. & Clobert, J. 1990. Tree community dynamics in a humid savanna of the Cote-d'Ivoire: Modelling the effects of fire and competition with grass and neighbours. *Journal of Biogeography* **17**: 471-481.

Meron, E., Gilad, E., Von Hardenberg, J., Shachak, M. & Zarmi, Y. 2004. Vegetation patterns along a rainfall gradient. *Chaos, Solitons and Fractals* **19**: 367-376.

Meinhardt, H. 1995. The algorithmic beauty of seashells. Springer-Verlag, Berlin, Germany.

Okali, D.U.U., Hall, J.B. & Lawson, G.W. 1973. Root distribution under a thicket clump on the Accra Plains, Ghana: Its relevance to clump localization and water relations. *Journal of Ecology* **61**: 439-454.

Olff, H., Vera, F.W.M., Bokdam, J., Bakker, E.S., Gleichman, J.M., De Maeyer, K. & Smit, R. 1999. Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation and competition. *Plant Biology* **1**: 127-137.

Ponce, V.M. & Da Cunha, C.N. 1993. Vegetated earthmounds in tropical savannas of Central Brazil: A synthesis: with special reference to the Pantanal do Mato Grosso. *Journal of Biogeography* **20**: 219-225.

Prins, H.H.T. & Van der Jeugd, H.P. 1993. Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology* **81**: 305-314.

Rietkerk, M., Boerlijst, M.C., Van Langevelde, F., HilleRisLambers, R., Van de Koppel, J., Kumar, L., Prins, H.H.T. & De Roos, A.M. 2002. Self-organization of vegetation in arid ecosystems. *American Naturalist* **160**: 524-530.

Rietkerk, M., Dekker, S.C., De Ruiter, P.C. & Van de Koppel, J. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. *Science* **305**: 1926-1929.

Roques, K.G., O'Connor, T.G. & Watkinson, A.R. 2001. Dynamics of shrub encroachment in an African savanna: Relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* **38**: 268-280.

Sankaran, M., Ratman, J. & Hanan, N.P. 2004 Tree-grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters* **7**: 480-490.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J. & Zambatis, N. 2005. Determinants of woody cover in African savannas. *Nature* **438**: 846-849.

Schenk, H.J. & Jackson, R.B. 2002. Rooting depths, lateral root spreads, and belowground/aboveground allometries of plants in water-limited ecosystems. *Journal of Ecology* **90**: 480-494.

Scholes, R.J. & Archer, S.R. 1997. Tree–grass interactions in savannas. *Annual Review of Ecology and Systematics* **28**: 517-544.

Scholes, R.J., Dowty, P.R., Caylor, K., Parsons, D.A.B., Frost, P.G.H. & Shugart, H.H. 2002. Trends in savannas structure and composition along an aridity gradient in the Kalahari. *Journal of Vegetation Science* **13**: 419-428.

Shea, R.W., Shea, B.W., Kauffman, J.B., Ward, D.E., Haskins, C.I. & Scholes, M.C. 1996. Fuel biomass and consumption factors associated with fires in savanna ecosystems of South Africa and Zambia. *Journal of Geophysical Research* **101**: 23551-23568.

Smit, C., Vandenberghe, C., Den Ouden, J. & Müller-Schärer, H. 2007. Nurse plants, tree saplings and grazing pressure: changes in facilitation along a biotic environmental gradient. *Oecologia* 10.1007/s00442-006-0650-6.

Turing, A.M. 1952. The chemical basis of morphogenesis. *Philosophical Transactions of the Royal Society of London, Series B – Biological Sciences* **237**: 37-72.

Van de Koppel, J. & Prins, H.T.T. 1998. The importance of herbivore interactions for the dynamics of African savanna woodlands: and hypothesis. *Journal of Tropical Ecology* **14**: 565-576.

Van de Koppel, J., Rietkerk, M., Dankers, N. & Herman, P.M.J. 2005. Scale-dependent feedback and regular spatial patterns in young mussel beds. *American Naturalist* **165**: E66-E77.

Van de Vijver, C.A.D.M., Foley, C.A. & Olff, H. 1999. Changes in the woody component of an East African savanna during 25 years. *Journal of Tropical Ecology* **15**: 545-564.

Van Langevelde, F., Van de Vijver, C.A.D.M., Kumar, L., Van de Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J., Prins, H.H.T. & Rietkerk, M. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**: 337-350.

Van Wijk, M.T. & Rodriguez-Iturbe, I. 2002. Tree-grass competition in space and time: Insights from a simple cellular automata model based on ecohydrological dynamics. *Water Resources Research* **38**: 1179-1193.

References to chapter 6

Beerling, D.J. & Osborne, C.P. 2006. The origin of the savanna biome. *Global Change Biology* **12**: 2023-2031.

Bergstrom, U., Englund, G. & Leonardsson, K. 2006. Plugging Space into Predator-Prey Models: An Empirical Approach. *American Naturalist* **167**: 246-259.

Bond, W.J. & Keeley, J.E. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* **20**: 387-394.

Bond, W.J., Woodward, F.I. & Midgley, G.F. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* **165**: 525-538.

Breshears, D.D. 2006. The grassland-forest continuum: trends in ecosystem properties for woody plant mosaics? *Frontiers in Ecology and Environmental sciences* **4**: 96-104.

Briggs, J.M., Knapp, A.K. & Brock, B.L. 2002. Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing Interactions. *American Midland Naturalist* **147**: 287-294.

Brown, J.R. & Carter, J. 1998. Spatial and temporal patterns of exotic shrub invasion in an Australian tropical grassland. *Landscape Ecology* **13**: 93-102.

Cameron, E.Z. & Du Toit, J.T. 2007. Winning by a neck: tall giraffes avoid competing with shorter browsers. *American Naturalist* **169**: 130-135.

Carmona-Moreno, C., Belward, A., Malingreau, J.P., Hartley, A., Garcia-Alegre, M., Antonovskiy, M., Buchshtaber, V. & Pivovarov, V. 2005. Characterising interannual variation in global fire calendar using data from Earth Observing satellites. *Global Change Biology* **11**: 1537-1555.

Carpenter, S.R., Ludwig, D. & Brock, W.A. 1999. Management of eutrophication for lakes subject to potentially irreversible change. *Ecological Applications* **9**: 751-771.

D'Odorico, P., Laio, F. & Ridolfi, L. 2006. A probabilistic Analysis of Fire-Induced Tree-Grass Coexistence in savannas. *American Naturalist* **167**: E79-E87.

De Ronde, C., Trollope, W.S.W., Parr, C.L., Brockett, B.H. & Geldenhuys, C.J. 2004. Fire effects on flora and fauna. (60-87) in: Goldhammer, J.G. and De Ronde, C. (eds.). Wildland Fire Management: Handbook for Sub-Sahara Africa. Global Fire Monitoring Centre, Freiburg.

Drent, R.H. & Prins, H.H.T. 1987. The herbivore as prisoner of its food supply. (133-149) in Van Andel, J., Bakker, J. & Snaydon, R.W. (eds.). Disturbance in grasslands; species and population responses. Dr. W. Junk Publishing, Dortrecht.

Dublin, H.T., Sinclair, A.R.E. & McGlade, J. 1990. Elephants and fire as causes of multiple stable states in the serengeti-mara woodlands. *Journal of Animal ecology* **59**: 1147-1164.

Fowler, C.W. 1987. A review of density dependence in populations of large mammals. (401-441) in Genoways, H.H. (ed.). Current mammalogy. Plenum press, New York.

Goheen, J.R., Young, T.P., Keesing, F. & Palmer, T.M. 2007. Consequences of herbivory by native ungulates for the reproduction of a savanna tree. *Journal of Ecology* **95**: 129-138.

Govender, N., Trollope, L.A. & Wilgen, B.W. 2006. The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology* **43**: 748-758.

Hanski, I. 1990. Density dependence, regulation and variability in animal populations. *Philosophical Transactions/Royal Society of London Biological Sciences* **330**: 141-150.

HilleRisLambers, R., Rietkerk, M., Van den Bosch, F., Prins, H.H.T. & Kroon, H. 2001. Vegetation pattern formation in semi-arid grazing systems. *Ecology* **82**: 50-61.

Hoffmann, W.A., Schroeder, W. & Jackson, R.B. 2002. Positive feedbacks of fire, climate, and vegetation and the conversion of tropical savanna. *Geophysical Research Letters* **29**: doi:10.1029/2002GL015424.

Illius, A.W. & O'Connor, T.G. 1999. On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications* **9**: 798-813.

Jackson, R.B., Canadel, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E. & Schulze, E.D. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* **108**: 389-411.

Janssen, M.A., Anderies, J.M. & Walker, B.H. 2004. Robust strategies for managing rangelands with multiple stable attractors. *Journal of environmental economics and management* **47**: 140-162.

Knoop, W.T. & Walker, B.H. 1985. Interactions of woody and herbaceous vegetation in a Southern African savanna. *Journal of Ecology* **73**: 235-253.

Knowlton, N. 1992. Thresholds and multiple stable states in coral reef community dynamics. *American Zoologist* **32**: 674-682.

Loth, P.E., De Boer, W.F., Heitkönig, I.M.A. & Prins, H.H.T. 2005. Germination strategy of the East African savanna tree *Acacia tortilis*. *Journal of Tropical Ecology* **21**: 509-518.

McNaughton, S.J. 1979. Grassland-herbivore dynamics. In Sinclair, A.R.E. & Norton-Griffiths, M. (eds.). Serengeti: Dynamics of an ecosystem. The University of Chicago Press, Chicago.

Nystrom, M., Folke, C. & Moberg, F. 2000. Coral reef disturbance and resilience in a human-dominated environment. *Trends in Ecology and Evolution* **15**: 413-417.

Owen-Smith, N. & Mills, M.G.L. 2006. Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. *Ecological Monographs* **76**: 73-92.

Owen-Smith, N. & Ogutu, J. 2003. Rainfall influences on ungulate populations dynamics. (310-330) in Du Toit, J.T., Rogers, K.H. & Biggs, H.C. (eds.). The kruger experience: ecology and management of savanna heterogeneity. Island press.

Prins, H.H.T. 1993. Productivity of tropical herbivore assemblages: Nature's basis for exploitation by man. EEAP publication: 67 Wageningen Pers. pp. 3-17.

Prins, H.H.T. & Van der Jeugd, H.P. 1993. Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology* **81**: 305-314.

Rietkerk, M., Dekker, S.C., De Ruiter, P.C. & Van de Koppel, J. 2004. Self-Organized Patchiness and Catastrophic Shifts in Ecosystems. *Science* **305**: 1926-1929.

Rietkerk, M. & Van de Koppel, J. 1997. Alternate stable states and threshold effects in semi-arid grazing systems. *Oikos* **79**: 69-76.

Roques, K.G., O'Connor, T.G. & Watkinson, A.R. 2001. Dynamics of shrub encroachment in an African savanna: relative influence of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* **38**: 268-280.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J. & Zambatis, N. 2005. Determinants of woody cover in African savannas. *Nature* **438**: 846-849.

Scheffer, M. & Carpenter, S.R. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution* **18**: 648-656.

Scheffer, M., Carpenter, S.R., Foley, J.A., Folke, C. & Walker, B.H. 2001. Catastrophic shifts in ecosystems. *Nature* **413**: 591-596.

Scheffer, M., Rinaldi, S., Gragnani, A., Mur, L.R. & Van Nes, E.H. 1997. On the dominance of filamentous cyanobacteria in shallow, turbid lakes. *Ecology* **78**: 272-282.

Schenk, H.J. & Jackson, R.B. 2002. Rooting depth, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology* **90**: 480-494.

Scholes, R.J. & Archer, S.R. 1997. Tree-Grass interactions in savannas. *Annual Reviews of Ecological Systems* **28**: 517-544.

Toulmin, C. 1994. Tracking drought: options for destocking and restocking. (95-115) in: Scoones, I. (ed.). Living with uncertainty; new directions in pastoral development in Africa. London.

Trollope, W.S.W., De Ronde, C. & Geldenhuys, C.J. 2004. Fire behaviour. (27-59) in: Goldhammer, J.G. & De Ronde, C. (eds.). Wildland Fire Management: Handbook for Sub-Sahara Africa. Global Fire Monitoring Centre, Freiburg.

Van Auken, O.W. 2000. Shrub invasions of north american semiarid grasslands. *Annual Review of Ecology and Systematics* **31**: 197-215.

Van de Koppel, J. & Rietkerk, M. 2000. herbivore regulation and irreverible vegetation change in semi-arid grazing systems. *Oikos* **90**: 253-260.

Van de Koppel, J., Rietkerk, M., Van Langevelde, F., Kumar, L., Klausmeier, C.A., Fryxell, J.M., Hearne, J.W., Van Andel, J., De Ridder, N., Skidmore, A.K., Stroosnijder, L. & Prins, H.H.T. 2002. Spatial heterogeneity and irreversible vegetation change in semiarid grazing systems. *American Naturalist* **159**: 209-218.

Van Langevelde, F., Van de Vijver, C.A.D.M., Kumar, L., Van de Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J., Prins, H.H.T. & Rietkerk, M. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**: 337-350.

Van Nes, E.H. & Scheffer, M. 2005. Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. *Ecology* **86**: 1797-1807.

Walker, B.H., Ludwig, D., Holling, C.S. & Peterman, R.M. 1981. Stability of semi-arid savanna grazing systems. *Journal of Ecology* **69**: 473-498.

Walker, B.H. & Noy-Meir, I. 1982. Aspects of the stability and resilience of savanna ecosystems. (556-590) in: Huntley, B.J. &Walker, B.H. (eds.). Ecology of Tropical Savannas. Springer Verlag, Berlin.

West, O. 1965. Fire in Vegetation and its use in Pasture Management; with special reference to tropical and subtropical Africa. Mimeographed Publication No.1/1965, Commonwealth Bureau of Pastures and Field Crops, CAB.

References to chapter 7

Belsky, A.J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology* **75**: 922-932.

Berjak, S.G. & Hearne, B.W. 2002 An improved cellular automaton model for simulating fire in a spatially heterogeneous savanna system. *Ecological modelling* **148**: 133-151.

Bond, W.J. & Van Wilgen, B.W. 1996. Fire and plants. Chapman & Hall, London. pp. 263.

Breshears, D.D. 2006. The grassland-forest continuum: trends in ecosystem properties for woody plant mosaics? *Frontiers in Ecology and Environmental sciences* **4**: 96-104.

Briggs, J.M., Knapp, A.K. & Brock, B.L. 2002. Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions. *American Midland Naturalist* **147**: 287-294.

Brockett, B.H., Biggs, H.C. & Van Wilgen, B.W. 2001. A patch mosaic burning system for conservation areas in southern African savannas. *International Journal of Wildland Fire* **10**: 169-183.

Brown, A.A. & Davis, K.P. 1973. Forest fire: control and use. McGraw Hill Book Co., New York. pp. 686.

Brown, J.R. & Carter, J. 1998. Spatial and temporal patterns of exotic shrub invasion in an Australian tropical grassland. *Landscape Ecology* **13**: 93-102.

Cain, M.L. 1990. Models of clonal growth in *Solidago altissima*. *Journal of Ecology* **78**: 27-46.

De Ronde, C., Trollope, W.S.W., Parr, C.L., Brockett, B.H. & Geldenhuys, C.J. 2004. Fire effects on flora and fauna. (60-87) in Goldhammer, J.G. & De Ronde, C. (eds.). Wildland Fire Management: Handbook for Sub-Sahara Africa. Global Fire Monitoring Centre, Freiburg.

Dublin, H.T., Sinclair, A.R.E. & McGlade, J. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology* **59**: 1147-1164.

Higgins, S.I., Bond, W.J. & Trollope, W.S.W. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* **88**: 213-229.

Jeltsch, F., Milton, S.J., Dean, W.R.J., Van Rooyen, N. & Moloney, K.A. 1998. Modelling the impact of small-scale heterogeneities on tree-grass coexistence in semi-arid savannas. *Journal of Ecology* **86**: 780-793.

Loth, P.E., De Boer, W.F., Heitkönig, I.M.A., Prins, H.H.T. 2005. Germination strategy of the East African savanna tree *Acacia tortilis*. *Journal of Tropical Ecology* **21**: 509-518.

Ludwig, F., De Kroon, H., Berendse, F. & Prins, H.H.T. 2004. The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant ecology* **170**: 93-105.

Owen, J.S. 1972. Fire Management in the Tanzania National Parks. *Proceedings of the Tall Timbers Fire Ecology Conference* **11**: 233-241.

Peters, D.P.C., Pielke Sr., R.A., Bestelmeyer, B.T., Allen, C.D., Munson-McGee, S. & Havstad, K.M. 2004. Cross-scale interactions, nonlinearities, and forecasting catastrophic events. *Proceedings of the National Academy of Sciences* **101**: 15130-15135.

Rietkerk, M., Boerlijst, M.C., Van Langevelde, F., HilleRisLambers, R., Van de Koppel, J., Kumar, L., Prins, H.H.T. & De Roos, A.M. 2002. Self organisation of vegetation in arid ecosystems. *American Naturalist* **160**: 524-530.

Rietkerk, M., Dekker, S.C., De Ruiter, P.C. & Van de Koppel, J. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. *Science* **305**: 1926-1929.

Roques, K.G., O'Connor, T.G. & Watkinson, A.R. 2001. Dynamics of shrub encroachment in an African savanna: relative influence of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* **38**: 268-280.

Rothermel, R.C. 1972. A mathematical model for predicting fire spread in wildland fuels. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT. Pap. INT-1 15. pp. 40.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J. & Zambatis, N. 2005. Determinants of woody cover in African savannas. *Nature* **438**: 846-849.

Scheffer, M., Carpenter, S.R., Foley, J.A., Folke, C. & Walker, B.H. 2001. Catastrophic shifts in ecosystems. *Nature* **413**: 591-596.

Schenk, H.J. & Jackson, R.B. 2002. Rooting depths, lateral root spreads, and belowground/aboveground allometries of plants in water-limited ecosystems. *Journal of Ecology* **90**: 480-494.

Scholes, R.J. & Archer, S.R. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* **28**: 517-544.

Trollope, W.S.W. 1998. Fire behaviour in African grasslands and savannas. Department of Livestock and Pasture Science, Faculty of Agriculture, University of Fort Hare, Alice, South Africa.

Van de Koppel, J. & Rietkerk, M. 2004. Spatial interactions and resilience in arid ecosystems. *American Naturalist* **163**: 113-121.

Van de Koppel, J., Rietkerk, M., Weissing, F.J. 1997. Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends in Ecology and Evolution* **12**: 352-356.

Van Langevelde, F., Van de Vijver, C.A.D.M., Kumar, L., Van de Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L.,

Bond, W.J., Prins, H.H.T. & Rietkerk, M. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**: 337-350.

Van Nes, E.H. & Scheffer, M. 2005. Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. *Ecology* **86**: 1797-1807.

Van Wijk, M.V. & Rodriguez-Iturbe, I. 2002. Tree-grass competition in space and time: insights from a simple cellular automata model based on ecohydrological dynamics. *Water Resources Research* **38**: 1179.

Vila, M., Lloret, F., Ogheri, E. & Terradas, J. 2001. Positive fire-grass feedback in Mediterranean Basin woodlands. *Forest Ecology and Management* **147**: 3-14.

Walker, B.H. & Noy-Meir, I. 1982. (556-590) in Huntley, B.J. & Walker, B.H. (eds.). Aspects of the stability and resilience of savanna ecosystems. Ecology of Tropical Savannas. Springer Verlag, Berlin.

Walter, H. 1971. Ecology of tropical and subtropical vegetation. Oliver & Boyd, Edinburgh, UK. pp. 539.

References to chapter 8

Archer, S.R., Scifres, C., Bassham, C.R. & Maggio, R. 1988. Autogenic succession in a Subtropical Savanna: Conversion of grassland to Thorn Woodland. *Ecological Monographs* **58**: 111-127.

Archibald, S, Bond, W.J., Stock, W.D. & Fairbanks, D.H.K. 2004. Shaping the landscape: fire–grazer interactions in an African savanna. *Ecological applications* **15**: 96-109.

Bond, W.J. & Keeley, J.E. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in ecology and Evolution* **20**: 387-394.

Bond, W. J., Midgley, G. F. & Woodward, W.I. 2003. The importance of low atmospheric CO2 and fire in promoting the spread of grasslands and savannas. *Global Change Biology* **9**: 973-982.

Bergström, U., Englund, G. & Leonardsson, K. 2006 Plugging space into predator-prey models: An empirical approach. *American Naturalist* **167**: 246-259.

Briggs, J.M., Knapp, A.K. & Brock, B.L. 2002. Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions. *American Midland Naturalist* **147**: 287-294.

Brown, J.R. & Carter, J. 1998. Spatial and temporal patterns of exotic shrub invasion in an Australian tropical grassland. *Landscape Ecology* **13**: 93-102.

Carmona-Moreno, C., Belward, A., Malingreau, J.P., Hartley, A., Garcia-Alegre, M., Antonovskiy, M., Buchshtaber, V. & Pivovarov, V. 2005. Characterising interannual variation in global fire calendar using data from Earth Observing satellites. *Global Change Biology* **11**: 1537-1555.

Carrick, P.J. 2003. Competitive and facilitative relationships among tree shrub species and the role of browsing intensity and rooting depth in the succulent Karoo, South Africa. *Journal of Vegetation Science* **14**: 761-772.

De Ronde, C., Trollope, W.S.W., Parr, C.L., Brockett, B.H. & Geldenhuys, C.J. 2004. Fire effects on flora and fauna. (60-87) in Goldhammer, J.G. & De Ronde, C. (eds.). Wildland Fire Management: Handbook for Sub-Sahara Africa. Global Fire Monitoring Centre, Freiburg. pp. 432.

De Roos, A.M. & Persson, L. 2002. Size-dependent life-history traits promote catastrophic collapses of top predators. *Proceedings of the National Academy of Sciences* **99**: 12907-12912.

Dublin, H.T., Sinclair, A.R.E. & McGlade J. 1990. Elephants and fire as causes of multiple stable states in the serengeti-mara woodlands. *Journal of Animal Ecology* **59**: 1147-1164.

Gierer, A. 1981. Generation of biological patterns and form: some physical, mathematical, and logical aspects. *Progress in Biophysics and Molecular Biology* **37**: 1-47.

Goheen, J.R., Young, T.P., Keesing, F. & Palmer, T.M., 2007. Consequences of herbivory by native ungulates for the reproduction of a savanna tree. *Journal of Ecology* **95**: 129-138.

Higgins, S.I., Bond, W.J. & Trollope, W.S.W. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* **88**: 213-229.

HilleRisLambers, R., Rietkerk, M., Van den Bosch, F., Prins, H.H.T., & De Kroon, H. 2001. Vegetation pattern formation in semi-arid grazing systems. *Ecology* **82**: 50–61.

Holmgren, M., Scheffer, M. & Huston, M.A. 1997. The interplay of facilitation and competition in plant communities. *Ecology* **78**: 1966-1975.

Jeltsch, F., Milton, S.J., Dean, W.R.J., Van Rooyen, N. & Moloney, K.A. 1998. Modelling the impact of small-scale heterogeneities on tree-grass coexistence in semi-arid savannas. *Journal of Ecology* **86**: 780-793.

Jeltsch, F., Weber, G.E. & Grimm, V. 2000. Ecological buffering mechanisms in savannas: A unifying theory of long-term tree-grass coexistence. *Plant Ecology* **161**: 161-171.

Klausmeier, C. A. 1999. Regular and irregular patterns in semiarid vegetation. *Science* **284**: 1826–1828.

Loth, P.E., De Boer, W.F., Heitkönig, I.M.A. & Prins, H.H.T. 2005. Germination strategy of the East African savanna tree Acacia tortilis. *Journal of Tropical Ecology* **21**: 509-518.

Meinhardt, H. 2003. The algorithmic beauty of sea shells. Springer, Germany.

Prins, H.H.T. & Van der Jeugd, H.P. 1993. Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology* **81**: 305-314.

Prins, H.H.T. 1996. Ecology and behaviour of the African buffalo, social inequality and decision making. Springen pp. 320.

Pyne, S.J., Goldammer, J.G., De Ronde, C., Geldenheys, C.J., Bond, W.J. & Trollope, W.S.W. Hominid hearth: An introduction to the human history of fire in Africa (1-10) in Goldhammer, J.G. & De Ronde, C. (eds.). Wildland Fire Management: Handbook for Sub-Sahara Africa. Global Fire Monitoring Centre, Freiburg. pp. 432.

Roques, K.G., O'Connor, T.G. & Watkinson, A.R. 2001. Dynamics of shrub encroachment in an African savanna: relative influence of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* **38**: 268-280.

Sala, O. E. *et al.* 2000. Biodiversity-global biodiversity scenarios for the year 2100. *Science* **287**: 1770-1774.

Scholes, R.J. & Archer, S.R. 1997. Tree-Grass interactions in savannas. *Annual Reviews of Ecological Systems* **28**: 517-544.

Scholes, R.J. & Walker, B.H. 1993. An African savanna: synthesis of the Nylsvley study. Cambridge University Press. Cambridge, UK.

Schröder, A., Persson, L. & De Roos, A.M. 2005. Direct experimental evidence for alternative stable states: a review. *Oikos* **110**: 3-19.

Scheffer, M. 1998. Ecology of shallow lakes. First edition. Chapman and Hall. London, UK.

Sharp, B.R. & Whittaker, R.J., The irreversible cattle-driven transformation of a seasonally flooded Australian savanna. *Journal of Biogeography* **30**: 783-802.

Sinclair, A.R.E. 1979. Dynamics of the Serengeti ecosystem. (1-30) in Sinclair, A.R.E. and Norton-Griffiths, M. (eds.). Serengeti: dynamics of an ecosystem. University of Chicago press, Chicago, Illinois, USA.

Smit, C., Den Ouden, J. & Müller-Schärer, H. 2006. Unpalatable plants facilitate tree sapling survival in wooded pastures. *Journal of Applied Ecology* **43**: 305-312.

Tilman, D., Lehman, C.L. & Kareiva, P. 1997. Population Dynamics in Spatial Habitats (3-20) in Tilman, D. and Kareiva, P. Spatial ecology; the role of space in population dynamics and interspecific interactions. Princeton university press, Princeton, New Jersey, USA. pp. 368 + xiv.

Tilman, D. & Kareiva, P. 1997. Spatial ecology; the role of space in population dynamics and interspecific interactions. Princeton university press, Princeton, New Jersey, USA. pp. 368 + xiv.

Tobler, M.W., Cochard, R. & Edwards, P.J. 2003 The impact of cattle ranching on large-scale vegetation pattern in a coastal savanna in Tanzania. *Journal of Applied Ecology* **40**: 430-444.

Van Auken, O.W. 2000. Shrub invasions of north american semiarid grasslands. *Annual Review of Ecology and Systematics* **31**: 197-215.

Van de Koppel, J. & Prins, H.H.T. 1998 The importance of herbivore interactions for the dynamics of African savanna woodlands: an hypothesis. *Journal of Tropical Ecology* **14:** 565-576.

Van de Vijver, C.A.D.M., Foley, C.A. & Olff, H. 1999 Changes in the woody component of an East African savanna during 25 years. *Journal of Tropical Ecology* **15**: 545-564.

Van Langevelde, F., Van de Vijver, C.A.D.M., Kumar, L., Van de Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J., Prins, H.H.T. & Rietkerk, M. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**: 337-350.

Van Nes, E.H. & Scheffer, M. 2005. Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. *Ecology* **86**: 1797-1807.

Van Wijk, M.V. & I. Rodriguez-Iturbe. 2002. Tree-grass competition in space and time: insights from a simple cellular automata model based on ecohydrological dynamics. *Water Resources Research* **38**: 1179.

Walker, B.H., Ludwig, D., Holling, C.S. & Peterman, R.M. 1981. Stability of semi-arid savannah grazing systems. *Journal of Ecology* **69**: 473-498.

Cover design: Thomas Groen & Job de Vogel
Printed by: Print Partners Ipskamp